Food or Habitat:
Drivers of *Diporeia* sediment preference on a Lake Superior transect

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Abstract

The amphipod *Diporeia* remains the dominant macroinvertebrate in Lake Superior despite drastic population declines throughout the rest of the Laurentian Great Lakes. Vital to the Lake Superior food web, *Diporeia* is most abundant in the slope region of the lake, at water depths between 30- and 125-meters. It has been hypothesized that this slope region is preferred because there are higher rates of both primary production and deposition in this zone, resulting in more food availability, but this hypothesis has not been directly tested. This study used 120-hour preference-avoidance bioassays to determine *Diporeia* sediment preference from different water depths along a transect. *Diporeia* strongly preferred sediment from 30- and 60-m water depth over deeper and shallower sites. Sediment from these two depths had significantly different chemical characteristics from each other, including total organic carbon, total nitrogen, and total phosphorus, which were used as indicators of food availability and quality. Of the variables tested, sediment grain size was the only variable that was consistent between the sites preferred by *Diporeia*, with both the 30- and 60-meter sites classified as predominantly medium silt and very poorly sorted. These results suggest that physical habitat may have a stronger influence on *Diporeia* habitat preference than food availability alone, arguing against food as a primary driver to *Diporeia* abundance patterns, and further suggesting dreissenid mussel's role as ecosystem engineers altering sediment grain size may have a role to play in *Diporeia* population decline.

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Introduction

The benthic amphipod *Diporeia* is often considered a keystone species in the Laurentian Great Lakes due to its historic abundance and important role in benthic-pelagic coupling (Auer et al., 2009). A keystone species is a species that has a disproportionately large effect on its ecosystem relative to its abundance (Montefalcone et al., 2011). Historically, *Diporeia* was one of the most ubiquitous benthic macroinvertebrates throughout the Great Lakes, accounting for more than 70% of benthic biomass (Cook & Johnson, 1974). As such, it was important prey for many Great Lakes fishes, including whitefish, lake trout, and sculpin (Nalepa et al., 2006).

Diporeia is a glacial relict formerly known as *Pontoporeia.* The *Pontoporeiidae* family was divided into three genera, including *Diporeia*, in 1989. Though other members of the *Pontoporeia* family can be found throughout the Holarctic, *Diporeia* is found only in deep North American glacial lakes (Bousfield, 1989). *Diporeia* is primarily found in the Laurentian Great Lakes and other lakes in the Canadian Precambrian Shield, though there are also some populations in lakes near the Pacific coast. It is not tolerant of brackish or saltwater (Bousfield, 1989). It is believed that there are four species of *Diporeia* in the Great Lakes, with *Diporeia hoyi* the most common (Bousfield, 1989; Pilgrim et al., 2009). However, *Diporeia* is generally referred to only by genus in the region. This is in part due to the difficulty of identifying individuals to species level, especially for females, which are collected in sampling surveys in much higher abundance than males (Bousfield, 1989; Pilgrim et al., 2009). Male *Diporeia* are undercounted because they have a much shorter lifespan than females and die after

mating. They are also found more often in the pelagic zone than females are (Bousfield, 1989). Notably, a DNA sequencing study found that Lake Superior's *Diporeia* population is also genetically distinct from the populations in the lower Great Lakes and may have diverged between 0.65 and 4.84 million years ago, before the formation of the Great Lakes as we know them today(Pilgrim et al., 2009).

Diporeia has a one- to two-year life cycle, which is largely dependent on water temperature (Balcer, 1984). At colder temperatures, like in the deep slope region of the Great Lakes, *Diporeia* generally has a two-year life cycle, while in warmer waters like the shallower shelf region of the Great Lakes or shallower lakes like Lake Washington its life cycle is only one year (Balcer, 1984; Evans et al., 1990; Green, 1968). *Diporeia* breeds in the winter (Evans et al., 1990) when short-lived males swim up into the water column simultaneously, followed by mature females (Bousfield, 1989). After mating, the males, which are primarily pelagic, die (Balcer, 1984; Green, 1968). Females survive months longer, releasing their eggs in the spring, resulting in distinguishable year classes (Balcer, 1984; Evans et al., 1990). A second mating event can occur in the summer with eggs released in late summer (Evans et al., 1990), though this second cohort has not been observed in Lake Superior (Auer et al., 2009). In deeper regions of the lake, it is possible for animals to have a three-year life cycle (Evans et al., 1990; Winnell & White, 1984).

These amphipods burrow in the top two centimeters of sediment and play a role in sediment bioturbation (Dermott & Corning, 1988). A two-centimeter bioturbation zone is shallower than the ten or more centimeter zone common in marine environments. Shallow bioturbation and a low sedimentation rate contribute to deeper oxygen penetration in Lake Superior sediment (3.5-12 cm) than marine sediment (a few

millimeters). This is because bioturbation transports organic material deeper into the sediment column which increases oxygen demand (Li et al., 2012).

While many amphipods are continuous feeders, *Diporeia* eats intermittently and selectively, taking advantage of high-quality diatoms when available. *Diporeia* is a deposit feeder and detritivore, relying on organic matter that settles out of the water column (Nalepa et al., 2005). *Diporeia* selectively consumes large diatoms of the genus *Stephanodiscus* and *Aulacoseira* in Lake Michigan when available, though its diet has shifted to smaller diatoms due to phytoplankton community changes after dreissenid mussel introduction (Edlund et al., 2021). Another Lake Michigan survey found that *Diporeia* guts are mostly full in the spring, with a smaller fullness peak in the fall. There is also a lower percentage of animals with empty guts during those time periods (Quigley, 1988). This seasonally intense feeding behavior is more pronounced in nearshore populations than those in deeper waters (Evans et al., 1990). Similar seasonal trends were also observed in Lake Ontario (Dermott & Corning, 1988). Given the timing of peak fullness during annual phytoplankton blooms, the percent of the population with full guts, and the long period of low fullness at other times of the year, *Diporeia* appears to take advantage of high-quality food available seasonally (Dermott & Corning, 1988; Quigley, 1988), One study indicated that they may be able to survive for as long as six months without food (Gauvin et al., 1989; Quigley, 1988). *Diporeia* is rich in lipids year-round but highest in lipid content in the spring(Gardner et al., 1985). So, *Diporeia* appears to exploit an annual spring diatom bloom when and where it occurs, obtaining a large portion of their energy with this high-quality food, then use lipid stores later in the year when only low-quality food is available (Dermott & Corning, 1988; Gardner et al., 1990).

Though it appears *Diporeia* preferentially consumes fresh diatoms when available, much of its diet is also composed of bacteria (Guiguer & Barton, 2002) and $\delta^{13}C$ values have indicated that benthic algae are also a significant portion of the diet of *Diporeia* in the photic zone in Lake Superior (Sierszen et al., 2006).

Much of the past work on *Diporeia* has been observational in nature. Laboratory experiments with wild-caught animals have largely focused on *Diporeia* consumption rates and its response to stressors. Early studies focused on *Diporeia* diet and ingestion rates by studying gut filling times (Dermott & Corning, 1988) and breakdown of diatoms (Quigley & Vanderploeg, 1991). Similar laboratory studies to identify consumption rates were performed by observing radiotracer uptake (Harkey et al., 1994) or fecal pellet production (Lozano et al., 2003). Corcoran et al. (2015) expanded this to study consumption rate under varying levels of food availability using radiolabeled algae, finding that *Diporeia* consumption rate follows a Michaelis-Menten saturation curve as animals are provided an increasing concentration of food. However, the maximum consumption rate (1.76 mgC/g dry weight/day) corresponds to a much higher carbon flux (1500-2000 $mgC/m^2/day$) than is typically seen in the Great Lakes (57-333 $mgC/m^2/day$), suggesting the animals typically exist at suboptimal food levels. Predicted consumption rates under Great Lakes sediment flux conditions are 0.08-0.38 mg C/g dry weight/day (Corcoran et al., 2015). Though this consumption rate of 0.1% dry body mass per day is low compared to other amphipods such as *Dikerogammarus villosus* (5-15%) (Richter et al., 2018) and macroinvertebrates like *Mysis mixta* (11-39%) (Rudstam, 1989) it is in line with previous studies of *Diporeia* feeding rate (Corcoran et al., 2015). These low

measured rates could be influenced by *Diporeia*'s intermittent feeding behavior (Lozano et al., 2003)

A few experiments have used RNA/DNA ratios as a proxy to investigate *Diporeia* growth. High RNA/DNA ratios suggest an organism is growing or has a greater growth potential (Chícharo & Chícharo, 2008). RNA/DNA ratios of Lake Michigan *Diporeia* decreased in response to short-term stress of transport from the field to the laboratory and were further depleted by the end of a 30-day starvation experiment, suggesting little growth during this food-limited period. A field portion of the same study reported RNA/DNA ratios of in situ *Diporeia* from throughout the Great Lakes but found no spatial or temporal environmental factors were able to explain the RNA/DNA differences in the field (Ryan et al., 2012). Kainz et al. (2010) performed a laboratory experiment looking at survivorship and RNA/DNA ratio in response to food quality. Of their four food treatments: *Ankistrodesmus falcatus, Microcystis aeruginosa,* mixed diatoms, and starvation, *Diporeia* had similar survival rates in all but Microcystis, where 0% survived. RNA/DNA ratios were highest in the diatom treatment and lowest in the starvation treatment, suggesting highest growth potential in diatom treatment (Kainz et al., 2010).

Experimental studies investigating *Diporeia*'s response to various stressors are another commonly performed laboratory experiment. Landrum et al. (2000) performed bioassays investigating *Diporeia* mortality and sediment preference using sediment collected from sites in Lake Michigan where *Diporeia* was absent. A 28-day mortality assay resulted in no significant mortality in any of the collected sediment, suggesting no acute toxins were present. They also used preference/avoidance bioassays, placing animals in a tank with petri dishes of sediment from different sites for 120 hours and

observed where *Diporeia* burrowed at the end of the period. They found that *Diporeia* did show preference, avoiding sediment from one site (St. Joseph) in favor of three other sites. *Diporeia* showed equal preference for sediment from the same sites that had been supplemented with diatoms, suggesting that food limitation may be a contributing factor in animal preference (Landrum et al., 2000). Assimilation and toxicity studies have been done exposing *Diporeia* to PAH and PCB (Harkey et al., 1994; Landrum et al., 1994, 2003), and the heavy metal cadmium (Gossiaux et al., 1992). *Diporeia*'s sensitivity to these compounds is similar to that of other amphipods (Landrum & Nalepa, 1998). *Diporeia'*s sensitivity to other stressors like salinity and temperature have also been tested in the laboratory (Gossiaux et al., 1992) where mortality was observed starting at 25 g sea salt/L in salinity tests and 24 hours at 28°C.

Diporeia is considered an integral part of the Great Lakes food web. They are lipid-rich, making them a particularly important prey species for fish (Gardner et al., 1990). *Diporeia* also plays a vital role in benthic-pelagic coupling by cycling energy from pelagic diatoms and other detritus that settle out of the water column back into higher trophic levels. One study estimated that *Diporeia* assimilates 60% of the organic carbon from the spring algal bloom in Lake Michigan (Fitzgerald & Gardner, 1993). These lipid-rich amphipods are important prey species for many Great Lakes fishes, particularly in the nearshore environment (Gamble et al., 2011; Sierszen et al., 2014), including sculpins, alewife, bloater, yellow perch, and rainbow smelt, and coregonines such as whitefish (Gamble et al., 2011; Nalepa et al., 2006). Approximately half of lake whitefish diet was *Diporeia* prior to *Diporeia* population declines (Pothoven & Madenjian, 2008), and whitefish growth rates have decreased in response (Rennie et al., 2009).

Once abundant in all the Great Lakes, *Diporeia* populations have declined in all except Lake Superior since the 1980s and 1990s (Auer et al., 2013; Barbiero et al., 2011; Nalepa et al., 2006). This decline was first observed in southern Lake Michigan (Nalepa et al., 1998) and the eastern basin of Lake Erie, where populations had decreased from 1840 individuals per m^2 to 220 per m^2 by 1993 (Dermott & Kerec, 1997). This trend has since spread to all lakes but Lake Superior. Surveys from the EPA's Great Lakes National Program Office have found that *Diporeia* was likely entirely gone in Lake Erie and nearly absent from sites shallower than 90m in Lakes Ontario, Michigan, and Huron (Burlakova et al., 2018). This contrasts with densities as high as 12,000 per m^2 in Lake Michigan nearshore in the 1980s (Nalepa et al., 1998). At sites deeper than 90m *Diporeia* was still present, but in lower densities than in the past: from 5,230 per m^2 (Dermott, 2001)to 96-198 per m^2 in Lake Ontario (Barbiero et al., 2011), from an average of about 4,000 per m^2 (Nalepa et al., 1998) to 57-1409 per m^2 (Barbiero et al., 2011) in Lake Michigan, and to 191-720 m^2 in Lake Huron(Barbiero et al., 2011).

Declines in *Diporeia* abundance have roughly coincided with the invasion by dreissenid mussels *Dreissena polymorpha* and *D. bugensis* into the Great Lakes. *D. polymorpha* was discovered in Lake St. Clair and Lake Erie in 1988 (Griffiths et al., 1991; Hebert et al., 1989) and had colonized the lakes by 1993 (Nalepa et al., 1998) Similarly, *D. bugensis* was discovered in Lake Erie in 1989 (Mills et al., 1993) and rapidly expanded, quickly colonizing Lakes Erie and Ontario (Mills et al., 1999), and with established populations in Lake Michigan discovered in 1997 (Nalepa et al., 2001).

The timelines of the dreissenid mussel invasion and beginning of *Diporeia*'s decline have led to a common, though contested, hypothesis that *Diporeia'*s decline is

due, at least in part, to interactions with dreissenid mussels. Competition with dreissenid mussels is one proposed interaction; mussels' filter feeding removes the seston settling out of the water column before it reaches *Diporeia*, resulting in food limitation (Dermott & Kerec, 1997; Nalepa et al., 1998). Shifts in *Diporeia* diet from larger and more preferred diatom species pre-invasion to smaller diatoms post-invasion support the hypothesis that *Diporeia* could be food limited (Edlund et al., 2021), though additional physical evidence of starvation is absent. Gauvin et al. (1989) found that *Diporeia* can survive for months without food by relying on their lipid stores, which decline during the starvation period (Gauvin et al., 1989). But during the *Diporeia* population decline in Lake Michigan, lipid levels and length-weight relationships remained stable, which would be unexpected if *Diporeia* was experiencing food scarcity(Nalepa et al., 2009). Alternative hypotheses about the role of dreissenids in *Diporeia* decline propose that dreissenids psuedofeces are toxic or have a negative effect on *Diporeia* (Dermott et al., 2005).

Several other observations contradict the hypothesis that the invasion of dreissenid mussels led to *Diporeia's* population decline. Population surveys in Lake Michigan showed areas where *Diporeia* and dreissenid mussels were both abundant, as well as areas where *Diporeia* was once abundant but is now absent without the presence of dreissenids (Nalepa et al., 2006). Similarly, *Diporeia* populations have not declined in New York's Finger Lakes, despite invasion by dreissenid mussels in the 1990s (Watkins et al., 2012). Finally, surveys have suggested that *Diporeia* population declines occurred around the same time in Lakes Michigan and Huron (early 2000s), even though only

Lake Michigan had a large established dreissenid population at that time (Barbiero et al., 2011).

Given their importance in the food web, top-down control by fish predation could also be driving *Diporeia* population decline. A few studies have shown that *Diporeia* population changes have coincided with changes in the fish community (Nalepa et al., 1998). Dermott (2001) noted that Lake Ontario's increase in whitefish population in the 1980s was a possible control on *Diporeia* population. However, this hypothesis seemed unlikely given that there was little change in the relative proportion of the population in each *Diporeia* size class and predation by whitefish would suggest a decrease in large individuals (Dermott, 2001). Similar analysis in Lake Michigan also indicated that fish predation was an unlikely driver of the pronounced decline in *Diporeia* population. Large declines in *Diporeia* populations occurred concurrently with a decline in yellow perch and relatively stable population of other fish predators (Nalepa et al., 1998). If *Diporeia* control was top-down, an increase in these fish species would be expected. Lake Superior *Diporeia* populations have increased since a 1974 survey (Cook, 1975), which corresponds with a decline in multiple benthivorous fish in the lake including slimy sculpin, burbot, and bloater (Scharold et al., 2004). Other proposed causes for *Diporeia* decline in the lower Great Lakes include viruses (Hewson et al., 2013) or other pathogens (Messick et al., 2004).

The dramatic shift in the macroinvertebrate community in the Great Lakes from *Diporeia* to dreissenid mussels is of ecological importance, regardless of the cause. *Diporeia* is important in benthic-pelagic coupling, while dreissenids are a poor food source for fish (Nalepa et al., 2009). Approximately 80% of dreissenids' dry biomass is

their shell (Nalepa et al., 2009; Roe & MacIsaac, 1997) which is of low nutritional value and has a high energetic cost to consume (Nalepa et al., 2009). Despite this, some species, like whitefish, have shifted their diets to dreissenids in response to the dramatic population changes (Madenjian et al., 2010; Pothoven & Nalepa, 2006).

Learning more about *Diporeia* habitat preference and feeding ecology is important, given *Diporeia's* role in the Great Lakes food web and the uncertainties around population declines. Several factors contribute to benthic macroinvertebrate habitat, including biotic (food availability, predation pressure) and abiotic (physical habitat, temperature, salinity, oxygen availability) forces. Animal fitness is connected to both the quantity and quality of food available, and there is evidence suggesting that *Diporeia* success is strongly tied to food, based on their intermittent feeding and reliance on diatoms when available. Food availability can be approximated by measuring the amount of organic carbon. Food quality can be measured in multiple ways including the source of organic carbon and the ratio of carbon to other essential nutrients, like nitrogen and phosphorus, which are often limiting in aquatic ecosystems (Hessen et al. 2013).

Substrate is also an important aspect of benthic habitats. Lacustrine sediment consists of a mixture of inorganic and organic particles and pore water. *Diporeia* is a burrower, and grain size and the amount of pore water can impact whether the animals are able to burrow. Grain size also has important implications for food availability for detritivores and deposit feeders. Not only do particles need to be of a certain size so that animals are able to consume them, but fine sediment often contains more organic matter and microorganisms, so food availability should vary with grain size (Levinton, 1995). Early studies in the Great Lakes did not find any correlation between *Diporeia* population

density and water depth, sediment particle size, or organic matter content in situ, but did find a correlation with bacterial density (Marzolf, 1965). Previous studies have shown that *Pontoporeia* in the Baltic Sea selectively consume sediment that is less than 10 µm (Ankar, 1977). Similarly, *Diporeia* also has been shown to prefer fine sediment, with sediment particles under 63 µm (Landrum & Faust, 1991) or 250 µm in diameter (Marzolf, 1965) preferentially ingested in previous experiments.

Despite their decline in the lower Great Lakes, *Diporeia* has remained the most abundant benthic macroinvertebrate in Lake Superior (Barbiero et al., 2011; Mehler et al., 2018; Scharold et al., 2009; Scharold & Corry, 2021), where they remain a vital part of the food web. *Diporeia*, along with the pelagic zooplankton *Mysis*, supports Lake Superior's food web, with *Diporeia* especially important in the near shore region (Gamble et al., 2011). *Diporeia* is so vital in Lake Superior that the Great Lakes Water Quality Agreement (GLWQA) uses *Diporeia* abundance as one of the indicators of ecological condition for the lake, calling for a density of 220-320 individuals/m^2 in nearshore areas (depths under 100 meters) and 30-160 individuals/m^2 in offshore (depths over 100m) (IJC, 1987; Scharold & Corry, 2021). A probability-based lake-wide survey conducted between 2006 and 2016 indicates that over three-quarters of Lake Superior meets these targets set by the GLWQA (J. v. Scharold & Corry, 2021).

The earliest survey of benthos in Lake Superior by Cook (1975) found a substantially lower density of *Diporeia* (243±55) than today. Differences in sampling techniques (Shipek grab vs. PONAR) and sampling season (spring vs. summer-late fall) may explain some of these differences (Scharold et al., 2004; Scharold & Corry, 2021), though additional explanations include a coinciding decrease in the population of

benthivorous fish such as slimy sculpin and ninespine stickleback (Bronte et al., 2003; Scharold & Corry, 2021) or a doubling of the diatom biomass from the 1970s to 2001 (Munawar & Munawar, 2009; Scharold & Corry, 2021).

The reason for *Diporeia*'s continued success in Lake Superior is unknown, as is the population's future. Dreissenids are not well established in the lake, with populations only observed in the Duluth-Superior Harbor (Grigorovich et al., 2008) and Apostle Islands National Lakeshore (Lafrancois et al., 2019). However, despite *Diporeia's* overall high abundance, a recent survey of nearshore monitoring stations found that population densities in 2016 (837 ± 132 per m^2) were the lowest it had been since 1994 (1937 ± 224 per m^2) (Mehler et al., 2018; J. V. Scharold et al., 2009). Historically, *Diporeia* densities have fluctuated greatly in Lake Superior, dipping in 2000 (1300 ± 250 per m^2) and rising again in 2003 (2050 ± 260 per m^2) (Scharold et al., 2009). So, there is uncertainty whether the low abundance in 2016 was the result of inter-annual variation or the first signs of the population decline observed in the lower Great Lakes (Mehler et al., 2018).

Previous studies have shown that *Diporeia* displays a unimodal abundance by depth in Lake Superior, with the highest density in the slope region between 30- and 125-meter water depth (Auer et al., 2013). This nearshore region generally has more primary production and more concentrated nutrients than the open lake (Howell et al., 2012; Makarewicz & Lewis, 2015; Sterner, 2021; Yurista et al., 2011). Deposition rates, measured by sediment traps, were also greater in this Keweenaw slope region than at nearby lakeward sites (Urban et al., 2004). Auer et al. (2013) called this region of high primary productivity and high deposition the "Ring of Fire", so coined because this depth region forms a ring around the lake and due to the abundance of *Diporeia* in this zone,

which accounts for less than one quarter of the lakebed area. They hypothesized that higher rates of pelagic primary production and subsequent deposition results in more food availability in this region, which promotes amphipod success (Auer et al., 2013). However, no study has yet directly tested the hypothesis that food availability in this region drives the population density.

This study investigated what factors contribute to *Diporeia* abundance in this slope region by investigating sediment characteristics and *Diporeia* preferences along a depth transect on Lake Superior's north shore. I collected animals and sediment from sites along this transect to perform laboratory bioassays observing *Diporeia* sediment choice along this depth gradient. I then characterized sediment from these sites based on physical (bulk density, sediment grain size) and chemical (loss on ignition, TOC, TN, TP, $\delta^{13}C$) characteristics to determine what factors contribute to *Diporeia* abundance. I hypothesized that *Diporeia* would prefer sediment from intermediate depths along the lake slope, and that preference would be related to measures of food quantity and quality.

Methods

Field Collections

Samples were collected from a transect on the north shore of Lake Superior (Figure 1) aboard the R/V *Blue Heron* and R/V *Kingfisher* over the summer of 2018 (May-October). The location of the transect was chosen due to its bathymetry, allowing for a large depth range to be sampled over a short distance (Figure 1, Table 1). The site was near the mouth of the French River in the Duluth sub-basin of Lake Superior. Overall, sediment in the Duluth sub-basin is characteristic of sediment throughout Lake Superior: predominantly clay, with a large proportion of silt and small component of sand. Sediment grains are coarser near the shore and become finer further offshore and inorganic carbon content is very small , less than 0.01% (Thomas & Dell, 1978).(Thomas & Dell, 1978). The sedimentation rate is higher in the Duluth sub-basin (0.025 g/cm^2/year) than in other areas of the lake because sediment from eroding Wisconsin lake bluffs enters the lake through the Duluth-Superior harbor (Corcoran et al., 2018; Kemp et al., 1978). My transect was on the northern shoreline of the Duluth sub-basin, where bedrock mountains and hills are thought to contribute a negligible input from erosion, especially when compared to the southern shore (Kemp et al., 1978).

Sediment and macroinvertebrate samples were collected with a PONAR grab sampler with a 0.052 m^2 surface area. PONAR surface screens were opened to collect undisturbed surficial sediment (top 2 cm) for chemical (TOC, TOC, TN, TP) and physical (bulk density, grain size) analysis, as well as for use in preference/avoidance assays.

Macroinvertebrate samples were also collected using a PONAR grab sampler. Samples were washed through a sediment elutriator (surface area approximately 0.25 m^2) with a 500μm (5/14-16/18, 6/5-7/18, 10/6/18) or 210μm (6/27/18, 7/17/18, and 8/14/18) net and *Diporeia* were transported back to the lab in 500mL bottles with lake water. Bottles were stored with lids off at 4°C in the dark until animals were released into preference/avoidance assays or analyzed for length/weight relationship and body composition analysis.

I was not able to conduct a rigorous abundance survey along this transect, due to time constraints. However, anecdotally, *Diporeia* was most abundant at the 30m and 60m site. There were moderate numbers at the 15m site. Deeper sites, (90, 120, and 150m) sites had very few *Diporeia* individuals, though at least one animal was seen at each location over the course of sampling.

Preference/Avoidance Assays

Five different 120-hour preference/avoidance assays were performed to observe *Diporeia* behavior and preference for sediment from different water depths, times of year, and differently aged sediment using similar methods to Landrum et al. (2000) (See Treatment Summaries). These tests assume that after 120 hours, *Diporeia* will have burrowed into the preferred and/or avoided the least preferred sediment options.

Sediment for preference/avoidance assays was homogenized manually while wet. In all trials there was a control of ashed beach sand collected from Park Point in Duluth, MN (46°46'17.3"N 92°05'13.7"W). Sediment was not pre-treated or filtered to remove

organic matter before use in preference/avoidance experiments unless otherwise noted in the treatment description.

For preference/avoidance tests, 6cm diameter petri-dishes were filled with an equal volume of sediment from given treatment (Table 2) and set on the bottom of a 56.8-liter glass tank filled to 10cm depth with 0.45 μm-filtered Lake Superior water. Tanks were aerated and kept at 4°C with no light for the duration of experiments.

Fifty *Diporeia* were released into the center of each tank and left for 120 hours. Animals caught in the surface tension were manually resubmerged during daily observations. After 120 hours, sediment dishes were removed, washed through a 500 μm sieve and the number of live burrowed individual *Diporeia* in each dish were recorded. Animals still swimming were not included in the analysis.

Occasionally more animals were recovered than were thought to be released (Table 2). This was likely because sediment was not pre-treated or filtered to remove organic matter so some animals already buried in this sediment may have been introduced. Therefore, I chose to include any such additional animals in our analysis. Similarly, in some tanks not all animals released were recovered. This was due to mortality or because not all the *Diporeia* were found burrowed after 120 hours. Unburrowed individuals could be seen swimming in the tank during dish removal but were not enumerated.

Treatment Summaries

Trial 1: Water Depth Alone (Trial 1A and 1B): The top 2 cm of sediment was collected from sites along a transect of water depth. Samples were taken at 15-, 30-, 60-, 90-, 120-,

and 150-meter water depth, at the coordinates found in Table 1. Two trials (1A and 1B) were run simultaneously in separate tanks. This test was run to determine whether *Diporeia* preferred sediment from any of the selected water depths along the transect.

Trial 2: Sediment Collected on Different Dates (Trial 2A and 2B): The top 2 cm of sediment was collected throughout the sampling season and frozen (Table 1). Sediment was then thawed before equal volumes were placed in each dish before trials. Two trials were performed at the same time, one tank with sediment from the 30m site (2A), and one with sediment from the 60m site (2B). This test was used to observe whether *Diporeia* preferred sediment from different times of year.

Trial 3: Water Depth and Sediment Depth combined: Sediment collected via PONAR was subsampled at 2cm intervals from surface to 6cm from 30 and 60m water depth, resulting in 3 sediment depth categories (0-2, 2-4, and 4-6 cm) for both 30 and 60m sites. This trial was done to investigate whether the age of sediment impacted *Diporeia* choice, or whether newly deposited sediment was preferred over older sediment.

Trial 4: Newly Deposited Sediment from Deeper Sites, and Older Sediment from Shallower Sites: 4-6cm sediment was used from 30 and 60m sites, while more recently deposited surficial sediment (0-2cm) was used from 90 and 150m sites for 4 different treatments (4-6cm sediment from 30m site, 4-6cm sediment from 60m site, 0-2cm sediment from 90m site, and 0-2cm sediment from 150m site). This trial investigated whether sediment age or site (water depth) had a stronger impact on *Diporeia* preference.

Trial 5: Food Subsidized Study: Commercial fish food (TetraMin® tropical flakes and Zoo Med Spirulina 20 fish food flakes) were added to 60m surficial sediment. Low food treatments contained 0.05mg dry weight of fish food and high food treatments contained 0.1mg. Quantity of food additions was determined after a previous pilot run with larger food additions. In this pilot study animals completely avoided the highest food additions (0.25mg) but did burrow in dishes with 0.1 and 0.05mg of added food. Food was mixed into the sediment manually until it appeared to be homogenous within the petri dish. This trial was used to look at whether food limitation seemed to be a factor in *Diporeia* preference. Both TetraMin® and Spirulina have been used in experiments or to rear *Diporeia* in the Great Lakes Environmental Research Laboratory (Landrum et al., 2000).

Sediment Chemistry

Surficial sediment samples from each sampling date and water depth were analyzed for loss on ignition, TOC, $\delta^{13}C$, TN, and $\delta^{15}N$, and TP. Upon return to the laboratory, all sediment for chemical analysis was frozen, freeze dried, and then homogenized with a mortar and pestle prior to analysis.

Loss on Ignition (LOI) was analyzed as an estimate for organic matter content (Schumacher 2002). Homogenized samples were subsampled and weighed on an analytical balance (to a target weight of 0.420-1.308 g). These samples were then heated

in a muffle furnace for 12 hours at 550°C. After cooling to room temperature, I again recorded the mass of the sample, and calculated the percent organic matter:

$$\frac{Initial\ Sample\ Weight - Final\ Sample\ Weight}{Initial\ Sample\ Weight} \times 100$$

Sediment Total Organic Carbon (TOC), Stable Carbon Isotopes ($\delta^{13}C$), Total Nitrogen (TN), and Nitrogen Isotopes ($\delta^{15}N$) were analyzed by EA-IRMS at the Large Lakes Observatory on a Finnegan Delta Plus XP isotope ratio mass spectrometer and using the Costech EA inlet. Standards used were acetanilide, caffeine, B-2153, and B-2159. Sediment subsamples were weighed, wrapped in Sn capsules, and analyzed for weight percent of TOC, $\delta^{13}C$, TN, and $\delta^{15}N$. Samples were not fumigated to remove carbonates prior to analysis, as a test run did not show a substantial difference in fumigated vs. non-fumigated samples suggesting a small percentage of carbonates. Past studies have also shown negligible inorganic carbon in Lake Superior sediment (Heinen & McManus, 2004; Li et al., 2012)(Heinen & McManus, 2004; Li et al., 2012). Therefore, all C measured in this way is referred to as organic. All samples were run in duplicate, with both values included in analysis.

Sediment Total Phosphorus (TP) was analyzed on SEAL AQ-400 Discrete Analyzer. Weighed sediment samples were ashed at 550°C for 2 hours. After cooling to room temperature 0.8mL of 10N H_2SO_4 was added to the sample and mixed, followed by 10mL of MQ water. Samples were then heated for 10 minutes at 100°C. After cooling back to room temperature, 2mL of molybdate reagent was added followed by 20 mL of

MQ water. Following digestions, samples were measured on a SEAL AQ-400 at 880 nm. All samples were run in duplicate, with both values included in analysis.

Sediment Physical Properties

Bulk Density. Sediment for bulk density was collected by PONAR on the same dates as sediment samples for experiments. A known volume of sediment was taken from the top 2 cm of the PONAR grab using a plastic syringe. Samples were frozen and freeze-dried, and the mass of dry sediment was divided by sediment volume to calculate bulk density. All samples were taken in triplicate except for the on the following dates: (6/7/18, 30m and 60m one additional sample was taken for 4 total replicates; 6/27/18, 150m had 1 sample only, 8/14/18, 150m had 2 samples only).

Grain size was analyzed on a Horiba Grain Size Analyzer LA-920 at LacCore in Minneapolis, MN. Sediment samples were stored at 4°C until pretreatment to remove organic matter and carbonates began.

To pretreat, approximately 5 cubic centimeters of sediment were placed in falcon tubes. Organic matter was removed using 30% H_2O_2. Samples were placed in a water bath heated to 85°C and 1mL H_2O_2 was added. Once reactions slowed, H_2O_2 was added in 2-5mL increments until a total of 30mL was added. After reactions had stopped, all samples were rinsed 3 times with 40 mL DI water by centrifuging samples at 3500 rpm for 20 minutes with DI rinse and then removing supernatant using a pipette sipper attached to a vacuum. Following this rinse carbonates were removed using a 10% HCl

solution. 1 mL of HCl was added to the homogenized sample at room temperature. Once the reaction stopped HCl was added in 2mL increments until a total of 5mL HCl was reached. The samples were again rinsed with DI water 3 times. Biogenic silica was not removed. All pretreatment was based on LacCore's standard operating procedures (Triplett and Heck, 2013). Following pretreatment all samples were analyzed on a Horiba Grain Size Analyzer LA-920.

Statistical Analysis

All statistical analyses were performed in RStudio (version 1.3.1093) unless otherwise noted (RStudio, 2020). I used two different approaches for statistical analysis in preference/avoidance experiments. First, because the data are fundamentally count data, I did loglinear modeling with expected values being equal across the table, adopting the framework for analysis provided by (Manly, 1993). I hypothesized that animals would not burrow randomly in preference avoidance tests ($p<0.05$). Models with more than one predictor variables were chosen based on Akaike information criterion (AIC), which penalizes for additional predictor variables (Quinn & Keough, 2003). I chose models with lower AIC, indicating a model with better fit.

The loglinear modeling approach provided an overall p-value for the test of non-independence in the data (i.e., whether *Diporeia* sorted by depth of sediment origin). More than 1 animal was expected to be burrowed in each dish for these tests. Though some authors caution against using this test where expected values are less than 5, this is because the tests become conservative with low sample size (Agresti,

2007). Given these concerns, I also performed a Kruskal-Wallis nonparametric test where each dish served as replicate within treatments. Kruskal-Wallis tests were followed with a Dunn test using the Bonferroni correction for multiple comparisons to determine which specific treatments were driving significance.

Loglinear modeling and the Kruskal-Wallis test have different strengths and weaknesses. Loglinear modeling is most appropriate for categorial multi-dimensional data and places more emphasis on individual data points, so outliers have a larger influence. Kruskal-Wallis, analogous to one-way ANOVA, is a nonparametric test for whether samples arise from the same population. Kruskal-Wallis compares ranked sums, so it is sensitive to the median values of groups. Loglinear models assume that counts within each cell follow a Poisson distribution. Kruskal-Wallis tests assume all groups come from an identically shaped and scaled distribution (though not necessarily normal), that differ only in their median. Neither statistical approach is clearly nor entirely correct in this application. Therefore, I interpreted the data using both approaches and have the greatest confidence in the conclusions when the two approaches agree.

For the water and sediment depth treatment I performed a series of 1-way Kruskal-Wallis nonparametric tests to test the interaction between water and sediment depth, as Kruskal-Wallis is unable to accommodate a factorial design.

A one-way ANOVA (α=0.05) was used to analyze sediment chemistry and bulk density data. Assumptions were met without transformations. Post-hoc Tukey HSD tests were run to determine differences between groups.

The GRADISTAT statistics package in Microsoft Excel was used to analyze grain size statistics including mean, median, mode, sorting, skew, kurtosis, D_{10}, D_{50}, and D_{90}

(Blott & Pye, 2001). D_{10}, D_{50}, and D_{90} are values that help describe the distribution of grain size, for example, D_{10} is the grain size where 10% of the material is finer. D_{50} is the median grain size and D_{16} and D_{84} show the grain sizes one standard deviation from the mean. GRADISTAT uses Folk and Ward's (1957) methods for calculating grain size summary statistics (Blott & Pye, 2001). Mean is calculated using the following equation:

$$Mean = \frac{D_{16} + D_{50} + D_{84}}{3}$$

Sorting is a commonly used measure of the variance of grain size within a sample that is able to incorporate the tails of the sample better than standard deviation alone (Folk & Ward, 1957). Well-sorted samples have a lower variance of grain size than poorly sorted samples. It is calculated using Folk and Ward's modified geometric method (1957) (Blott & Pye, 2001):

$$Sorting = \exp\left(\frac{\ln D_{16} - \ln D_{84}}{4} + \frac{\ln D_5 - \ln D_{95}}{6.6}\right)$$

GRADISTAT also classifies the sample by overall texture based on the percentage of the sample that falls into various grain size classifications using Folk's (1954) classification system. Skew is a measure of how asymmetrical the grain size curve is. A negative skew means the tail of the curve is coarser grains (i.e., there are more fine sediment grains) while a positive skew indicates the opposite (Folk & Ward, 1957).

$$Skewness = \frac{\ln D_{16} + \ln D_{84} - 2(\ln D_{50})}{2(\ln D_{84} - \ln D_{16})} + \frac{\ln D_5 + \ln D_{95} - 2(\ln D_{50})}{2(\ln D_{25} - \ln D_5)}$$

Kurtosis is used to describe the shape of a distribution relative to a normal. A value closer to 1 is more normal, with values greater than 1 generally more peaked and values lower than 1 flatter. Kurtosis is another measure of how grain sizes are sorted, with values

greater than 1 more poorly sorted than values less than 1, which would have more outliers (Folk & Ward, 1957).

$$Kurtosis = \frac{\ln D_5 - \ln D_{95}}{2.44(\ln D_{25} - \ln D_{75})}$$

Finally, the cumulative percentage curve is used to determine D_x, which gives the grain size for which x percent of grains are finer. So, for example, 10% of grains are finer than the D_{10}.

Results

Preference/Avoidance

All statistics for preference/avoidance experiments were performed both with and without ashed sand control. In all cases if the threshold for significance (α=0.05) was met with the control it was also met without the control, and vice versa. Because of these congruent results, all preference/avoidance statistics are reported in this section without the control.

Trial 1: Water Depth Alone.

Trial 1 was used to determine whether *Diporeia* preferred sediment from a particular water depth. Preference/avoidance tests using surficial sediment from each of the six sites along the transect were run in two separate tanks (Tank 1A and 1B, Figure 2). Experiments in the two tanks were run simultaneously and with the same conditions, including using sediment and animals collected on the same day. Analyzed independently, loglinear modeling suggested that animals did not burrow at random in one of the tanks (1A, $p<0.001$), while there was no evidence of preferential burrowing in the other (1B, $p=0.10$). This could reflect the conservative nature of the long-linear model with low expected values or result from the large number of zero counts and high variance within cells. In contrast, the Kruskal-Wallis tests suggested animals did not burrow at random in both tanks (1A, $p=0.0011$; 1B, $p=0.0032$) (Table 3). The most

notable differences between the two trials are that 1B had more individuals found burrowed in 15 m sediment than 1A (Figure 2).

However, AIC suggested that water depth alone was the most parsimonious predictor of *Diporeia* choice (AIC = 86.93) (Table 4). Therefore, I eliminated models including tank as a factor and combined data from trials 1A and 1B ("Trial 1"). Analyzing the combined dataset, both loglinear ($p=0.0013$) and K-W ANOVA ($p<0.001$) show that *Diporeia* did not burrow in sediment randomly (Table 3). More *Diporeia* were found burrowed in sediment from 30 and 60m water depth over deeper and shallower sites (Figure 3, Table 5, $\chi^2 = 38.147$, df=5, $p<0.001$). The control (ashed beach sand) as well as sediment from sites at or deeper than 90m were avoided completely, with no animals found burrowed in those dishes. Some individuals were found burrowed in the 15m sediment (mean = 0.88 ± 1.4), but significantly fewer than 60m (mean = 7.5 ± 7.2), and fewer than 30m (mean = 4.0 ± 3.0) (Table 5). There was a large variance in the number of individual *Diporeia* in the dishes in which they were found, particularly the 60m dish (2-22 individuals/dish, mean = 7.5 ± 7.2) (Figure 3).

Trial 2: Sediment Collected on Different Dates.

Diporeia did not show a clear preference for sediment collected on different dates, though different statistical approaches yielded somewhat different interpretations (Figure 4). According to Kruskal-Wallis tests ($p=0.58$ for 2A, $p=0.95$ for 2B, Table 6) there was no preference detected. However, loglinear modeling provided some evidence that *Diporeia* did not choose dishes randomly ($p=0.039$ for 2A, $p<0.001$ for 2B, Table 6).

There was large variance in the number of animals found burrowed between replicates for select months, with June in the 60m trial (Trial 2B) as the most extreme example, with 1 individual in the least populated dish, and 13 individuals in the most (Figure 4B). Evidence for seasonal preferences thus was equivocal. Selection based on season was weak to absent.

Trial 3: Water Depth and Sediment Depth combined.

The experiment looking at recently deposited sediment (0-2cm sediment depth) vs. older sediment (2-4 and 4-6cm sediment depth) suggested *Diporeia* may not be burrowing at random, but results were not entirely consistent statistically. The best fit model was with an interaction between site depth and sediment depth, which indicated that animals were not burrowing randomly (AIC=81.94, $p<0.001$, Table 7). However, when a 1-way Kruskal-Wallis test was performed, sediment depth alone influenced *Diporeia* dish choice ($p=0.047$, Table 8), not the interaction between water and sediment depth ($p=0.12$, Table 8). Significantly more *Diporeia* were found burrowed in the most recently deposited surficial sediment (0-2cm) than sediment that was 2-4cm deep (Figure 5, $p=0.042$, Table 9). Though not statistically significant, there were also more animals burrowed in surficial sediment than sediment 4-6cm deep ($p=0.057$, Table 9)

Trial 4: Newly Deposited Sediment from Deeper Sites, and Older Sediment from Shallower Sites.

Previous trials clearly showed that *Diporeia* preferred sediment from the 30 and 60m sites and suggested that they may prefer newly deposited to older sediment. This trial was used to investigate this further and determine whether the preference for sediment from shallower water depth was impacted by sediment age. Site was more important in *Diporeia* choice than sediment age. Older sediment (4-6cm sediment depth) from the two shallower sites (30m and 60m) was preferred over surficial sediment from deeper sites (90 and 150m) (Figure 6). Both loglinear modeling ($\chi^2 = 60.036$, df = 20, $p<0.001$) and K-W tests ($\chi^2 = 10.93$, df = 3, p=0.012) show that *Diporeia* do not burrow at random. However, pairwise tests between treatments did not show significant differences between groups, though the p-value between groups with older and newer sediment were low (Table 10).

Trial 5: Food Subsidized Study.

Diporeia did not show evidence of preference in the food addition preference/avoidance assay. The interaction between the type of food added (TetraMin® vs. Spirulina 20) and the amount (0.05 vs. 0.1mg) was the best fit loglinear model to explain *Diporeia* burrowing (AIC=39.63, Table 11). Both loglinear modeling and Kruskal-Wallis test suggested that additional food does not have a significant influence on *Diporeia* preference for 60m sediment (Figure 7, loglinear modeling p=0.28, Table 11, K-W ANOVA p=0.88, Table 12).

Summary of Preference/Avoidance Assay Results

Overall, preference/avoidance tests indicated that *Diporeia* shows a strong and consistent preference for sediment from 30 and 60m water depth over deeper and shallower sites. Animals prefer recently deposited surficial sediment over older, deeper sediment, but preference for site location is stronger than that for sediment age. Some evidence was found that *Diporeia* preferred sediment from early in the summer season, but this conclusion was not clear cut. There was little to no evidence to support the hypothesis that animals prefer sediment with supplemented food.

Sediment Chemistry

Surficial sediment from the 15 and 30m sites had lower organic content than deeper sites (Figure 8). LOI was used as an estimate of organic content in surficial sediment samples. LOI was significantly different between the shallow (15 and 30m) and deep sites (60 through 150m) (1-way ANOVA, $F = 16.76$, df. = 5, $p < 0.0001$), therefore deeper sites along the transect (60m and deeper) had higher percent organic content than these shallower sites (Figure 8, Table 13).

TOC (Figure 9A), and TN (Figure 9B) in sediment samples showed a similar pattern to LOI, with the shallower 15 and 30m sites having significantly lower weight percent C (1-way ANOVA, $p<0.0001$) and N (1-way ANOVA, $p<0.0001$) than deeper sites (Table 14-15). TP (1-way ANOVA, $p<0.0001$) was also lowest in the two shallowest sites, but percent TP at 60m is more intermediate (Figure 9C, Table 16). The date the sample was collected did not have a significant effect on TOC, TN, or TP, as

evidenced by 1-way ANOVA using water depth, collection date, as well as the interaction term ($p = 0.175$ for TOC, $p = 0.171$ for TN, $p = 0.12$ for TP). Overall, sites do have significantly different sediment chemistry, with significantly higher percent organic carbon, TOC, TN, and TP at the deeper sites (60-150m) than the shallow sites (15 and 30m).

Sediment C:N ratios were consistent across all depths (1-way ANOVA, $p=0.102$) while C:P ($p<0.001$) and N:P ($p<0.001$) ratios were significantly smaller at 15 and 30m water depth than at deeper sites (Figure 10, Table 17-18). $\delta^{13}C$ (1-way ANOVA, $p<0.0001$) became steadily more depleted as sites deepen and get further from shore (Figure 11), with sites 90m and deeper significantly more depleted than 60m and shallower (Table 19).

Bulk Density and Grain Size Analysis

Bulk density was significantly different between depths (1-way ANOVA, $p<0.001$). The shallower 15 and 30m sites had significantly higher bulk density than deeper sites (Figure 12, Table 20).

All sample sites were primarily composed of silt with a mode grain size of 14.21μm. The 15-60m sites were dominated primarily by medium silt, while the 90m and deeper sites were dominated by fine silt. All samples were poorly sorted except for 30 and 60m sites, which were very poorly sorted, with a larger spread of grain sizes (Table 21, Figure 13). In general, there was a larger percentage of large particles at sites that were shallower and closer to shore (D_{90}) (Table 21).

Overall Summary

Results from preference-avoidance assays indicated that *Diporeia* preferentially burrowed in surficial sediment from 30 and 60 m water depth. However, the sediment chemistry from these two sites did not set them apart from the other locations along the transect. . These two water depths did not share similar amounts of carbon, nitrogen, or phosphorus, with 30m site having significantly less of all three elements than the 60m site, though $\delta^{13}C$ was similar at both the 30 and 60m site. The same pattern held for bulk density, with the 30m site having significantly higher bulk density than the 60m site. Grain size, on the other hand, did show some similarities between 30 and 60m sediments, and that those two depths differ from other depths. Both the 30 and 60m sites were primarily medium silt but are very poorly sorted while other sites are poorly sorted.

Discussion

Preference-avoidance assays demonstrated that *Diporeia* collected from a depth transect in Lake Superior showed strong preference for sediment from intermediate water depths, supporting one of the main hypotheses of this study. This pattern of preference aligns with known regions of greatest *Diporeia* population density in Lake Superior, which shows abundance peaks between 20- and 65-meter water depth (Auer et al., 2013; Auer et al., 2009; Auer & Kahn, 2004; Barbiero et al., 2011; Kraft, 1979; Scharold & Corry, 2021). Similar regions of high abundance have been noted throughout the Great Lakes since as early as the 1930s (Auer et al., 2013), including high density regions between 30 and 50 meters in Lake Michigan (Nalepa, 1989; Nalepa et al., 2000, 2005), between 30 and 90 meters in Lake Huron (Dobiesz et al., 2005) and between 31 and 36 meters in Lake Ontario (Sly & Christie, 1992). Though quantitative abundance data were not collected during this study, the 30- and 60-meter sites were also where *Diporeia* appeared to be most abundant along the studied transect.

The other hypothesis, that *Diporeia* preference would correspond with indicators of food availability or higher quality food, was not supported. TOC along the study transect was greater at the sites in water 60 meters or deeper compared to the 15- and 30-meter sites (Figure 9, Table 14). This is consistent with studies demonstrating that organic content increases as particle size decreases, which occurs when moving lakeward into less turbulent regions. (Auer et al., 2013; Thomas & Dell, 1978). Sediment TN and TP showed similar patterns, with a significantly higher percentage of TN and TP at the deeper sites (60-meters and greater) than shallower (15- and 30-meter sites) (Figure 10,

Tables 15 and 16). $\delta^{13}C$ values also differed by depth, steadily becoming more depleted as depth increased (Figure 11). This suggests that the form of sediment organic carbon is shifting along the gradient moving lakeward, though the cause is unclear. Differing $\delta^{13}C$ values can indicate different carbon sources, and more depleted $\delta^{13}C$ can indicate more autochthonous carbon sources than allochthonous, suggesting more terrestrial organic matter in the nearshore environment. However, the $\delta^{13}C$ composition of freshwater algae (-24 to -30‰) overlaps with that of C3 terrestrial plants (-23 to -26‰), (Bianchi & Canuel, 2011; Meyers, 1997) making distinguishing between allochthonous and autochthonous carbon sources challenging in freshwater environments. Additionally, though the $\delta^{13}C$ can indicate the source of carbon, it can also be connected to lipid content, with lipids having more negative $\delta^{13}C$ values (Masclaux & Richoux, 2017), so it is possible the deeper sites with more depleted $\delta^{13}C$ are richer in lipids.

Regardless, *Diporeia* preference does not appear to follow carbon, nitrogen, or phosphorus patterns alone. If *Diporeia* was primarily cueing into food or nutrient availability, I would expect them to prefer sediment from sites 60m and deeper, but animals also showed a strong preference for sediment from the 30-meter site. This suggests that food is not the main driver of *Diporeia* habitat preference and thus, presumably, distribution.

This study did find that sediment grain size corresponded with *Diporeia* preference. Sediments from both 30- and 60-meter sites were primarily medium silt, but were very poorly sorted, so there was a large variance of grain sizes (Figure 13, Table 21). Though they were the richest in total carbon, phosphorus, and nitrogen, the poorly

sorted, fine silt sites at 90-meter water depth and deeper were entirely avoided in laboratory preference-avoidance experiments (Trial 1, Figure 2).

Auer et al. 2013 hypothesized that *Diporeia* abundance was concentrated in a "ring of fire" on the slope of Lake Superior that corresponded to a zone of "transitional deposition". They proposed that this transitional region is uniquely located near areas where shallower nearshore regions with high primary productivity but also high resuspension rates, meet the less productive and less turbulent profundal lake. Therefore, this zone is depositional, but with higher food availability (Auer et al., 2013). However, evidence for the cause of the "ring of fire" is circumstantial and exact cause remains unknown. The present study is the first direct test of *Diporeia* sediment preference along a depth gradient and it found that *Diporeia* does show a strong preference for sites that correspond to the same depth range as the "ring of fire." This implies that something about or in the sediment at those sites is appealing to *Diporeia*. Sediment chemistry and physical analysis suggest that sediment grain size (physical habitat) may be more important than food availability or quality alone in *Diporeia* habitat selection and distribution. This is not to say that food availability is irrelevant, but rather that other factors such as physical habitat may be a stronger driver in habitat choice than previously thought.

Sediment grain size can affect physical habitat characteristics important to the burrowing *Diporeia*. Both the amount of pore water and sediment grain size influence sediment texture, which can influence how easily macroinvertebrates can burrow, including burrowing rate and depth (Nel et al., 2001; Sun et al., 2019). Cummins and Lauff (1969) found that the distribution of benthic macroinvertebrates in stream

environments was influenced by several factors. While temperature, current velocity, and chemical parameters (like pH and oxygen saturation) determined if a habitat was tolerable, substrate particle size and food availability determined macroinvertebrate distribution within suitable habitat (Cummins & Lauff, 1969). Other studies have found that benthic macroinvertebrate species richness is higher in heterogenous sediment in riverine environments (Beisel et al., 1998), and species richness and abundance is highest in coarse sediment in groundwater aquifers (Korbel et al., 2019). Korbel also found that amphipods preferred course sediment to clay and were unable to burrow into clay sediment in their experiment. The pore spaces in clay sediment were found to be small enough that animals were unable to move between interstitial spaces and had to actively dig to move through the sediment (Korbel et al., 2019). Sediment grain size and substrate preferences are dependent on the species.

Sediment grain size may also be more important than food availability due to *Diporeia's* ability to feed intermittently. Rich lipid stores mean that animals can survive for long periods of time without significant food, as evident by exploitation of the spring diatom bloom in Lake Michigan (Dermott & Corning, 1988; Gardner et al., 1990). However, the correspondence to Lake Superior which lacks similar seasonality in diatom production is questionable. If animals are relying on internal energy stores in times of low food availability, other pressures, like physical habitat, may be more important in habitat selection.

Sediment grain size is not completely disconnected from dietary needs. Amphipods are gape-limited, meaning they are only able to consume what they can fit in their mouth (Smith & Petranka, 1987). Previous studies have suggested that *Diporeia*

prefer to consume fine sediment particles with a diameter less than 63 µm (Landrum & Faust, 1991) or 250 µm (Marzolf, 1965). However, all the sites in this study, other than the beach sand control, had both mean and mode sediment grain size under the 63 µm threshold, suggesting that there is abundant size-appropriate sediment for *Diporeia* consumption at all sites. Grain size is also correlated with organic matter content, as there is also often more organic matter in finer sediment (Thomas, 1969), which is supported in this study, as the sites at 60 meters and deeper do have a smaller mode grain size (14.21 and 0.627 µm) higher organic carbon content, and more depleted $\delta^{13}C$ values than shallower sites. Though organic carbon content was removed from samples before grain size analysis, it is likely that organic and inorganic particles settling in the same area would be of similar mass and size.

Though this study did not find a strong indication that food availability influenced *Diporeia* sediment preference, food availability or quality may still be a factor in habitat selection. This study used unspecific measures for food availability (loss on ignition and TOC in sediment) as well as for food quality (TN and TP). These measures are imperfect, for example sediment TP and TN include inorganic fractions, so the values measured here are not all available as food sources. In addition, each sediment chemistry measurement represents one moment in time, so does not show the flux of carbon through the system. Given the high density of amphipods at some sites, it is possible that newly deposited organic matter is quickly consumed, so the carbon observed during any one measurement would not capture a high rate of carbon flux (Auer et al., 2013). Simply measuring sediment chemistry also does not describe the lability of the carbon, and whether it is easily consumed and able to be converted to energy. Finally, as described

earlier, *Diporeia* prefer to consume sediment of a certain size range, so animal selection based on grain size may be in part due to food availability, in that they select habitat with sediments of a particular grain size because they are easier to consume.

There was not a clear pattern in *Diporeia* preference for sediment from different times of the year (Trial 2). The contradictory statistical results between loglinear modeling and Kruskal-Wallis show the different emphasis placed by each test (Table 6). Loglinear modeling places more emphasis on individual data points, in this case represented by dishes, and so outliers have a larger influence. It appears that while the overall difference between groups is small (Kruskal-Wallis test), the large variance in the number of animals found burrowed in dishes (see the June 60m trial for an example, Figure 4B), skews the loglinear modeling analysis. Therefore, there is some evidence that *Diporeia* burrowed non-randomly in this trial, but there is no clear pattern in *Diporeia* preference for sediment from different times of the year. Given previous studies demonstration that *Diporeia* can gain a significant portion of its annual energy during the spring diatom bloom (Dermott & Corning, 1988; Gardner et al., 1990), I assumed that *Diporeia* would select sediment from warming summer months, June and July when primary production may be greater. Sediment trap studies along the Keweenaw Peninsula have shown that carbon and nitrogen concentration is slightly higher when Lake Superior is stratified than when it is unstratified (Urban et al. 2004). However, the oligotrophic Lake Superior does not have the same large spring phytoplankton bloom that was characteristic in the Lower Great Lakes prior to the invasion of dreissenid mussels, so may not have the same seasonal delivery of high energy detritus. Recent studies have shown that annual chlorophyll a levels in Lakes Huron and Michigan are now similar to

those in Lake Superior, suggesting that Lake Superior's primary production is similar to that of the lower Great Lakes post dreissenid invasion, without a pronounced phytoplankton bloom (Fahnenstiel et al., 2016; Sterner, 2010). Sediment was also frozen between collection and when the experiment was run in November, which could have altered any algae cells present. For example, studies from Belgium found that abruptly freezing freshwater diatom samples to -20°C was lethal to most diatom strains (Souffreau et al., 2010), so freezing the sediment may have killed any diatoms present which may affect Diporeia preference

The test comparing recently deposited sediment compared to older sediment (Trial 3) also produced some contradictory results. There was some evidence that sediment depth alone influenced *Diporeia* choice (Kruskal-Wallis), and other evidence suggesting the interaction between site and sediment depth is the best fit model (loglinear modeling). More *Diporeia* were found burrowed in the most recently deposited surficial sediment (0-2cm) at both the 30 and 60m site (Figure 5, Table 9), though only the comparison between sediment 0-2cm deep and 2-4cm deep was statistically significant.

In multiple trials, there was a large range of individuals found burrowed between replicates, (in different dishes of sediment from the same site or treatment). For example, between 2 and 22 individuals burrowed in dishes with 60m sediment in Trial 1, and between 0 and 15 individuals burrowed into dishes of the same treatment in Trial 3. This raises the question whether there is any herding behavior among *Diporeia*, or whether there is another social cue impacting animal preference. Otherwise, I might expect lower variance. This observation could suggest that there is an advantage to a higher density of *Diporeia*, such as for protection from predation or reproduction.

Explanations of how dreissenid mussels may be contributing to *Diporeia* population declines are usually focused on competition, hypothesizing that *Diporeia* may be food-limited due to changes in the phytoplankton community, or because preferred food is filtered out of the water column before it reaches the lakebed. Dreissenid mussels' impact on increasing water clarity and decreasing chlorophyll levels has long been studied, but they also have an impact on physical habitat. Dreissenid shells cover the lakebed when animals are in high abundance, which both stabilizes sediment, and creates a hard substrate. Their filtering process is not selective, as dreissenids filter particles larger than 0.4µm, though they are selective in which size fraction they consume, preferentially selecting particles between 15 and 40µm in laboratory experiments (Karatayev et al., 2002; ten Winkel & Davids, 1982). This range is consistent with the sediment grain size of sites preferred by *Diporeia* in this experiment. Observations from a site in eastern Lake Erie near the Niagara River also indicated that sediment grain size shifted from 1988 to 1992 as dreissenid mussel populations increased at the site. Between 1988 and 1991 sediment had a median grain size of 125-200µm (fine sand) but this size decreased to 4-7µm (silt) by 1992 (Howell et al., 1996). This was hypothesized to be in part due to dreissenid psuedofeces, which has been shown to be less than 10µm in diameter (Reeders & Bij de Vaate, 1992; Howell et al., 1996). Given *Diporeia*'s preference for sediment with a mix of fine sand and silt particles shown in this study, this shift to clay and silt could have a large impact on *Diporeia* habitat if this pattern is seen elsewhere in the Great Lakes. The role of mussels as ecosystem engineers, altering the physical habitat and sediment grain size should continue to be investigated, to see whether physical habitat changes may be able to help explain *Diporeia* decline.

Diporeia is a key species in Lake Superior and the Laurentian Great Lakes, so much so that it is included as an indicator of ecosystem health in the Great Lakes Water Quality Agreement (IJC, 1987; Scharold et al., 2004). Its population decline in the lower Great Lakes has caused major concern due to its importance in the food web as well as its role in bioturbation, and therefore oxygen penetration in Great Lakes sediment. Despite *Diporeia's* importance, much about this animal is still unknown. This study demonstrates the importance of physical habitat, specifically sediment grain size, in *Diporeia* habitat preference. Given the strong relation of *Diporeia* to its physical habitat revealed in this study, hypotheses about how invasive species affect native benthic species through altering the nature of sediment characteristics have increased importance, and shifts in physical habitat post dreissenid invasion may be worth investigating when considering causes for the dramatic decline in *Diporeia* population in the lower Great Lakes

Figures and Tables

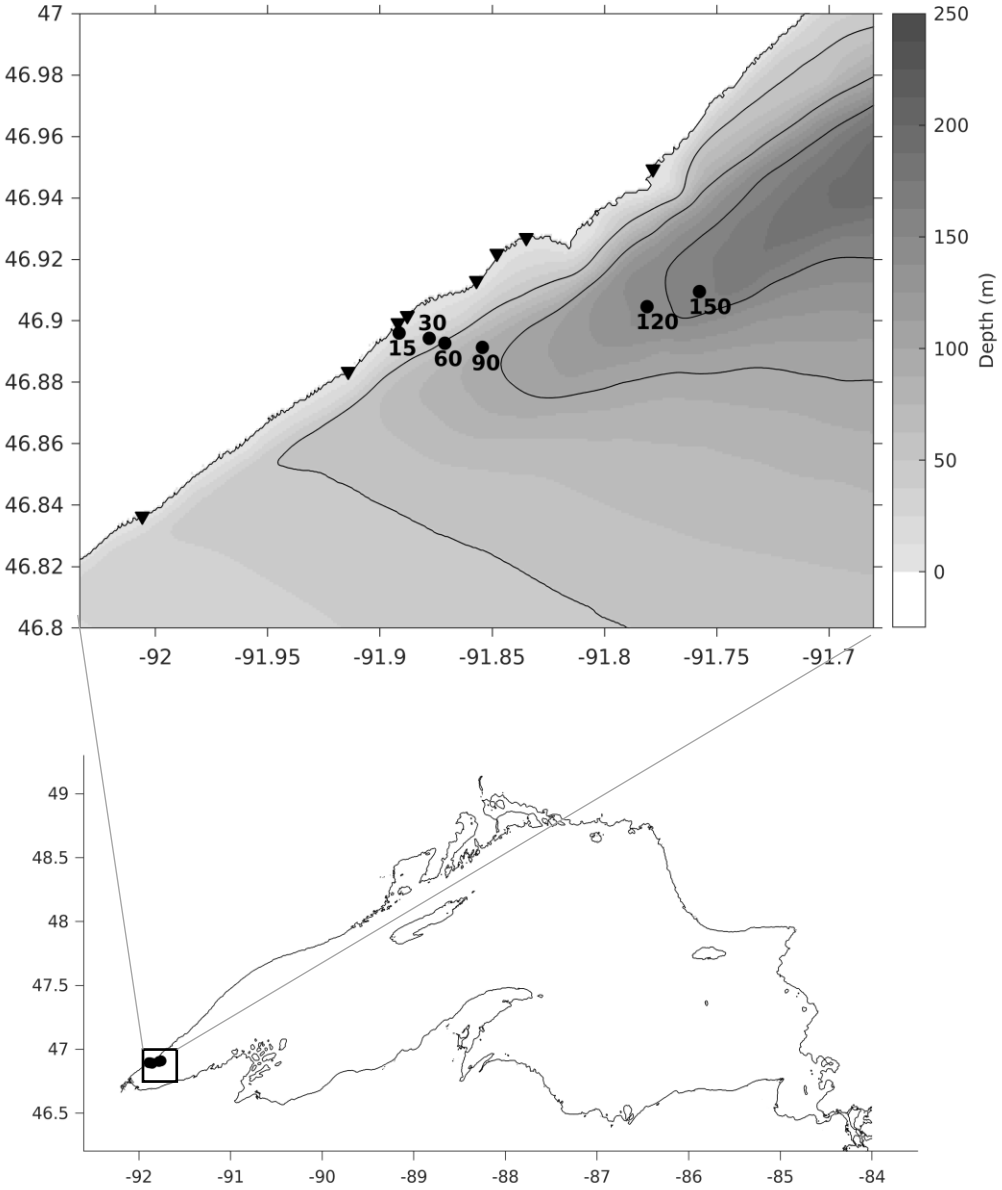

Figure 1. Sampling locations on the North Shore of Lake Superior. Contour lines are at 50, 100, 150m water depth. Black triangles indicate the mouth of major rivers and streams.

Table 1. Coordinates of sampling locations and 2018 dates when sediment was collected. *Diporeia* for experiments were collected on the same dates, primarily from 30 and 60m water depths, with some from 15m site.

Depth (m)	GPS Coordinates	5/14	5/16	6/5	6/7	6/27	7/17	8/14	10/6
15	46º 53.760 N; 91º 53.491 W	X			X		X	X	
30	46° 53.659 N; 91°52.685 W	X			X	X	X	X	
60	46° 53.559 N; 91°52.270 W	X	X	X	X	X	X	X	X
90	46° 53.479 N; 91°51.261 W		X	X			X	X	
120	46° 54.278 N; 91°46.863 W		X	X					
150	46° 54.572 N; 91°45.461 W		X	X		X		X	

Table 2. Summary of preference/avoidance trials performed over the summer of 2018.

Trial ID	Trial Name	Date experiment ended	Number of replicates per treatment	Number of *Diporeia* released	Number of live *Diporeia* recovered
1A	Water Depth (Tank A)	6/20/2018	4	50	52
1B	Water Depth (Tank B)	6/20/2018	4	50	47
2A	Seasonal (30m sediment)	11/16/2018	3	47	29
2B	Seasonal (60m sediment)	11/16/2018	3	50	40
3	Water Depth and sediment depth	8/22/2018	4	50	44
4	Fresh sediment (deeper sites), older sediment (shallower sites)	8/22/2018	6	50	41
5	Food Supplement	8/22/2018	5	50	39

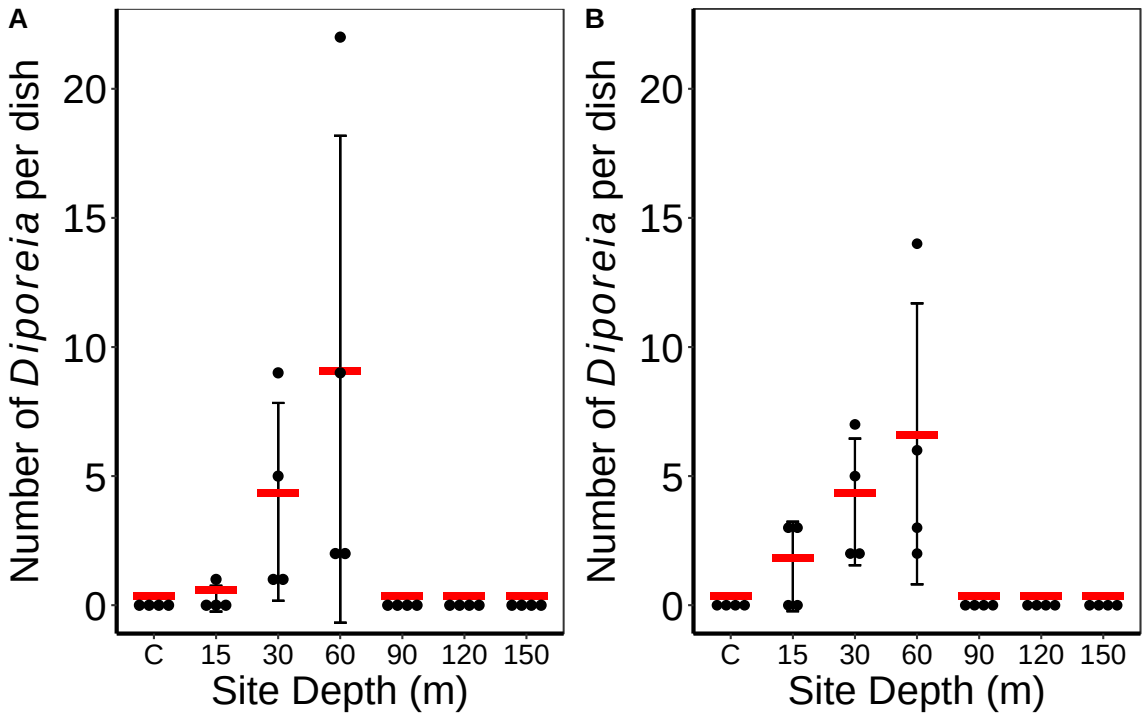

Figure 2. Number of *Diporeia* burrowed in surficial sediment from given depths from A. Trial 1A and B. Trial 1B. Here and elsewhere, points represent one petri dish, red dashes represent the mean and whiskers are ± 1 sd.

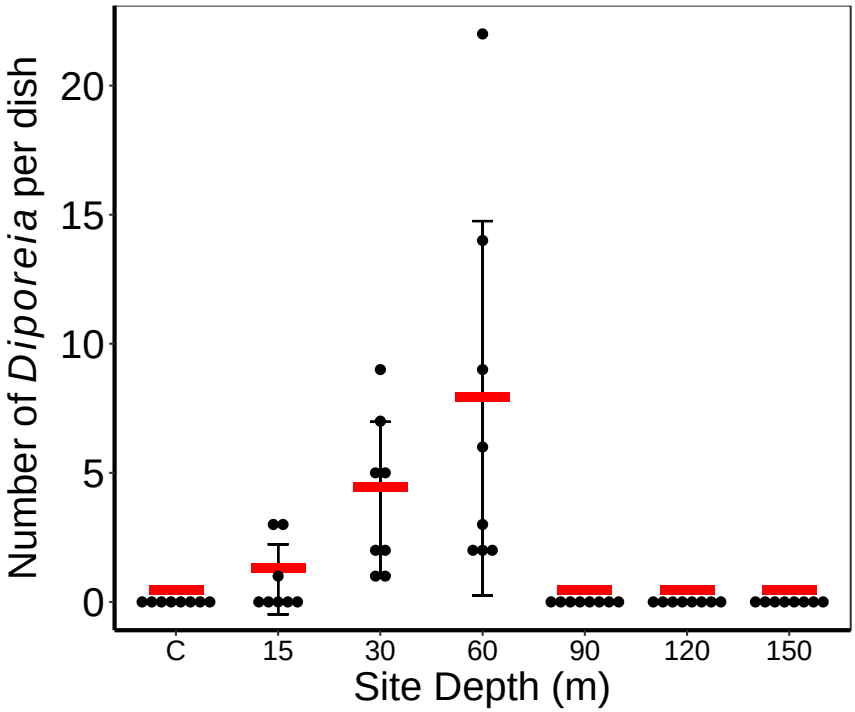

Figure 3. Number of *Diporeia* by depth of sediment from water surface from Trial 1 (Tanks A and B combined).

Table 3. Summary statistics (loglinear and Kruskal-Wallis ANOVA) for all models without control included.

		Loglinear modeling			Kruskal-Wallis ANOVA		
Trial ID	Model	χ^2	d.f.	p	χ^2	d.f.	p-value
1A	Tank A only	43.32	18	**<0.001**	20.357	5	**0.0011**
1B	Tank B only	25.97	18	0.10	17.817	5	**0.0032**
1	Tank A and B combined	74.93	42	**0.0013**	38.147	5	**<0.001**
	Depth+Tank Combined*	74.68	41	**0.0010**			
	Depth*Tank Combined*	69.29	36	**<0.001**			

Table 4. AIC values from loglinear modeling statistics used to select model with best fit.

Model	AIC
Depth * tank	93.29
Depth + tank	88.68
Depth only	86.93

Table 5. Multiple comparisons between 30- and 60-meter sediment (columns) and all others (rows) from post-hoc Dunn test following Kruskal-Wallis ANOVA on Tank A and B combined (Trial ID 1), including and excluding controls.

Depth (m)	30	60
15	0.11	**0.028**
30		1
60	1	
90	**0.0014**	**<0.001**
120	**0.0014**	**<0.001**
150	**0.0014**	**<0.001**

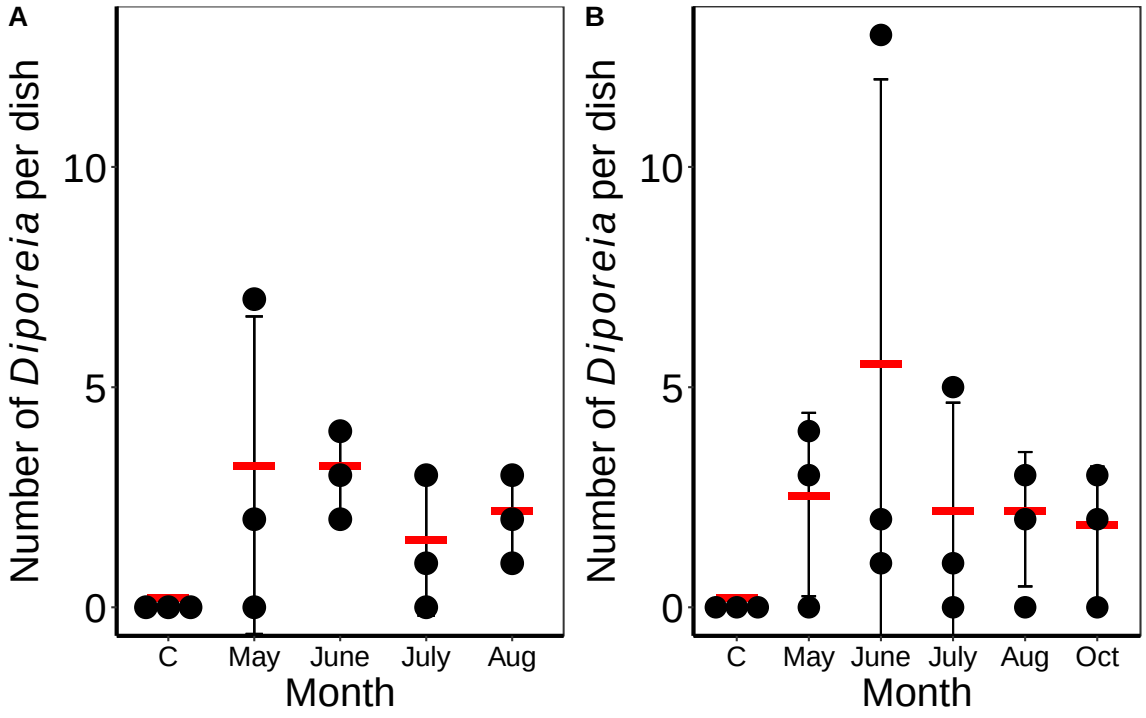

Figure 4. Number of *Diporeia* burrowed in dishes full of surficial sediment from given months. A. 2A (30m sediment) and B. 2B (60m sediment) from the given months.

Table 6. Summary statistics without control. χ^2 values represent likelihood ratio.

		Loglinear modeling			Kruskal-Wallis ANOVA		
Trial ID	Model	χ^2	d.f.	p	χ^2	d.f.	p-value
2A	30m sediment	16.26	8	0.039	1.95	3	0.58
2B	60m sediment	38.00	10	<0.001	0.74	4	0.95

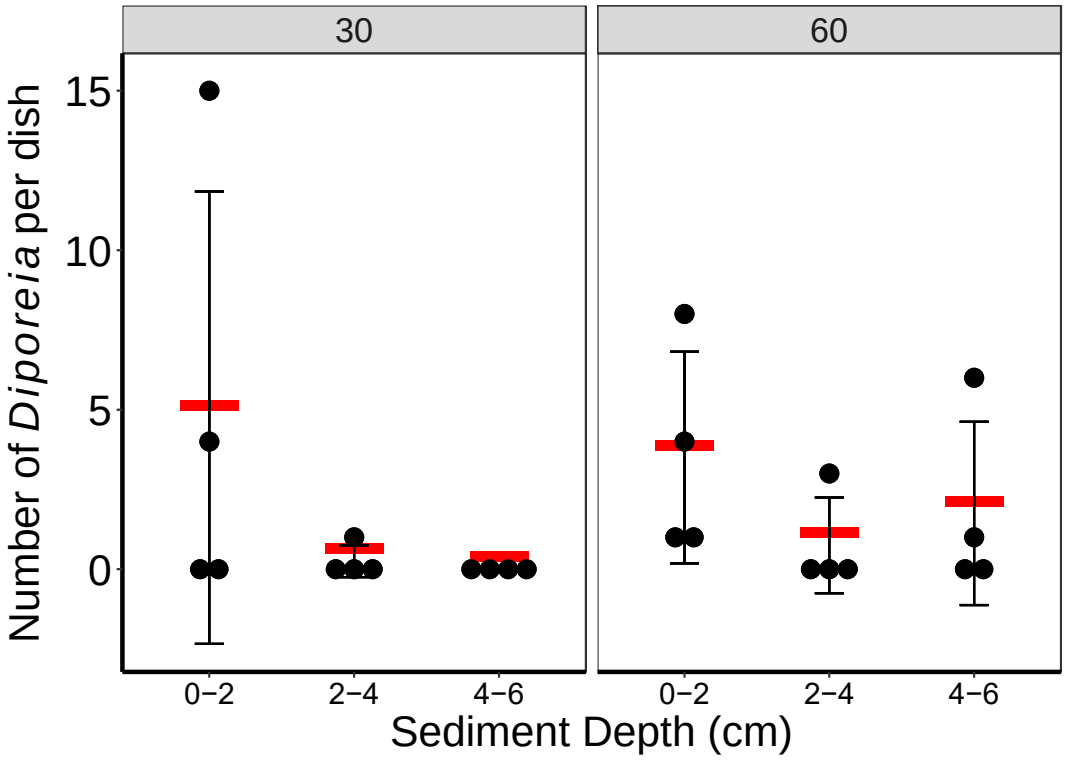

Figure 5. Trial 3. Number of *Diporeia* burrowed in surficial sediment from given water depth and sediment depth. 30m site in left panel; 60m site in right panel.

Table 7. Loglinear modeling statistics used to select model with best fit, controls not included.

Model	χ^2	d.f.	p-value	AIC
Water Depth + Sediment Depth	81.77	20	<0.001	89.77
Water Depth * Sediment Depth	69.94	18	<0.001	81.94
Sediment Depth only	82.33	21	<0.001	88.33

Table 8. Statistics from Kruskal-Wallis ANOVA, controls not included

Model	χ^2	d.f.	p-value
Sediment Depth	6.11	2	0.047
Water Depth	1.93	1	0.16
Water Depth*Sediment Depth	8.77	5	0.12

Table 9. Results of Dunn-test for multiple comparisons after Kruskal-Wallis test (Controls not included)

Comparison		P-value (adjusted)
0-2	2-4	0.042
0-2	4-6	0.057
2-4	4-6	1.0

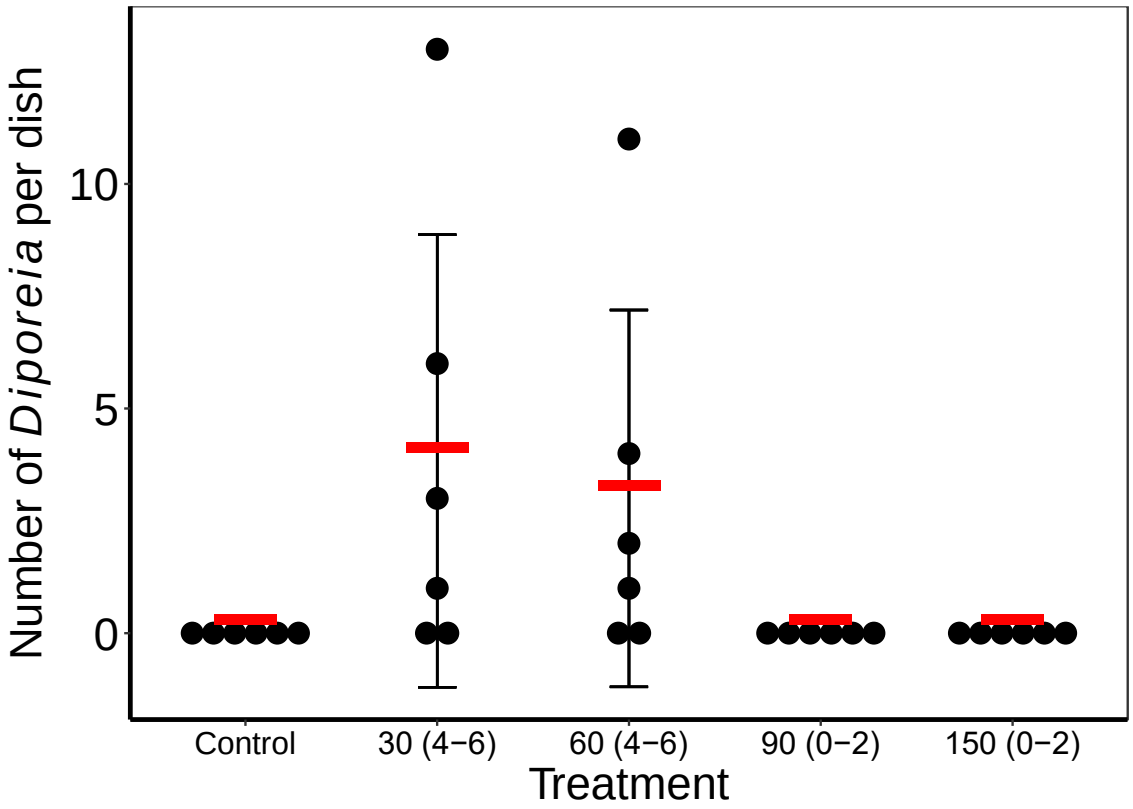

Figure 6. Trial 4. Number of *Diporeia* burrowed in sediment from the given water (and sediment) depth.

Table 10. Results of Dunn-test for multiple comparisons after Kruskal-Wallis test for trial 4. (Controls not included)

Depth (m)	30 (2-4)	60 (2-4)	90 (0-2)
60 (2-4)	1		
90 (0-2)	**0.048**	0.071	
150 (0-2)	**0.048**	0.071	1

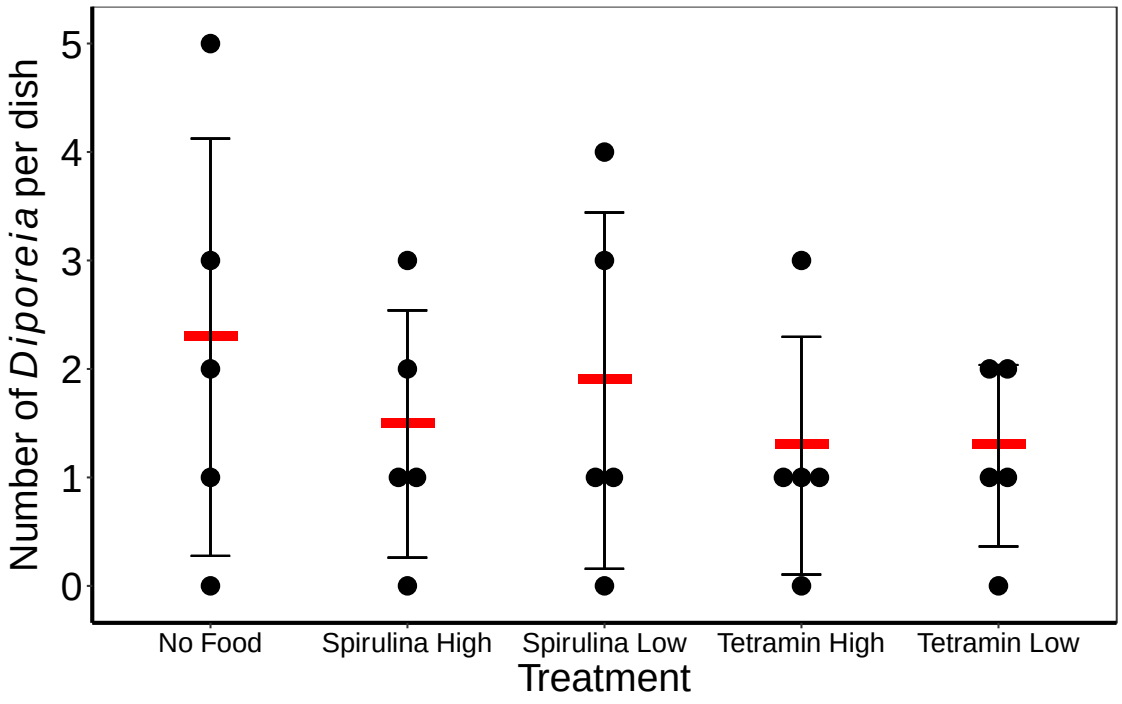

Figure 7. Trial 5. Number of *Diporeia* burrowed in surficial sediment with given food additions. Low treatments had 0.05mg of food added to 28.21 mL of sediment while high treatments had 0.1mg of food added.

Table 11. Loglinear modeling statistics used to select model with best fit, controls included.

Model	χ^2	d.f.	p-value	AIC
Food Type + Amount	41.03	26	0.031	49.03
Food Type * Amount	27.63	24	0.28	39.63
Amount only	42.08	28	0.043	46.08

Table 12. Statistics from Kruskal-Wallis ANOVA, controls excluded.

Model	χ^2	d.f.	p-value
Food Type * Amount	1.19	4	0.88
Amount only	0.87	2	0.65
Food Type only	1.09	2	0.58

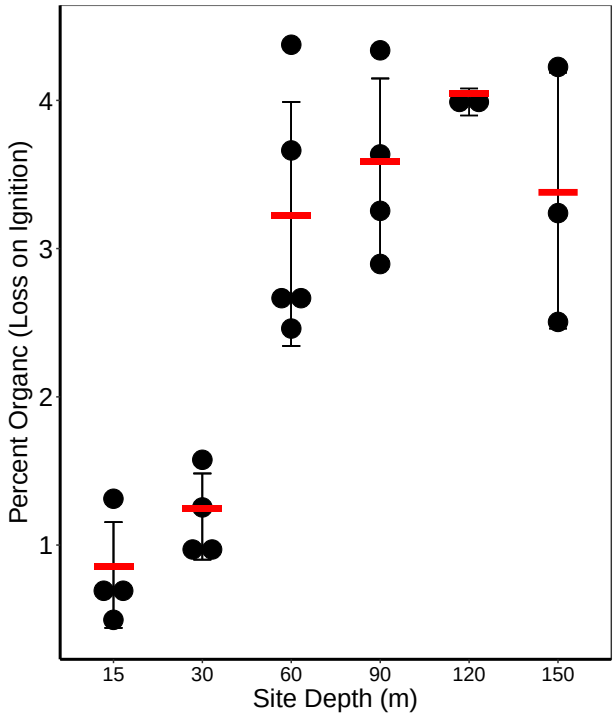

Figure 8. Percent loss on ignition in surficial sediment sample (0-2cm) from given water depth determined by loss on ignition. Points represent 1 replicate, red dashes represent the mean, and whiskers are 1 standard deviation from the mean.

Table 13. Results of Tukey HSD pairwise tests for LOI.

	15	30	60	90	120
30	0.94				
60	**0.0003**	**0.0022**			
90	**0.00012**	**0.00069**	0.94		
120	**0.00022**	**0.00088**	0.6	0.95	
150	**0.00069**	**0.0036**	1	1	0.83

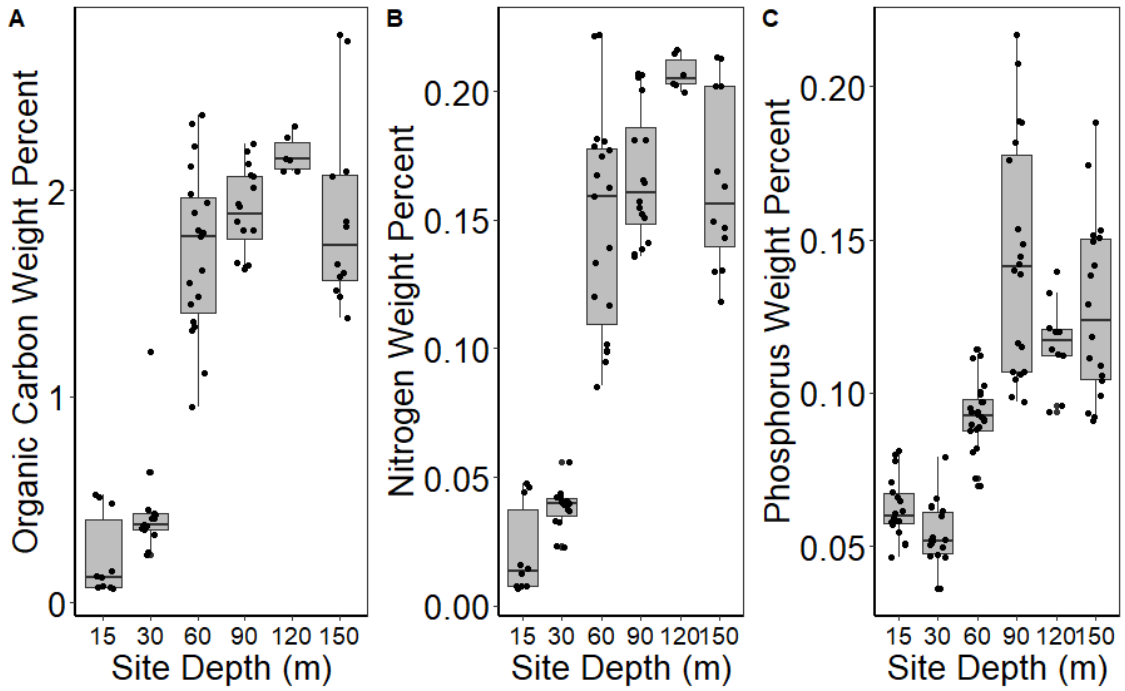

Figure 9. Sediment chemistry by site depth. A. Percent TOC B. Percent TN C. Percent TP. Boxplots show median and 25% quartiles. Points represent individual samples.

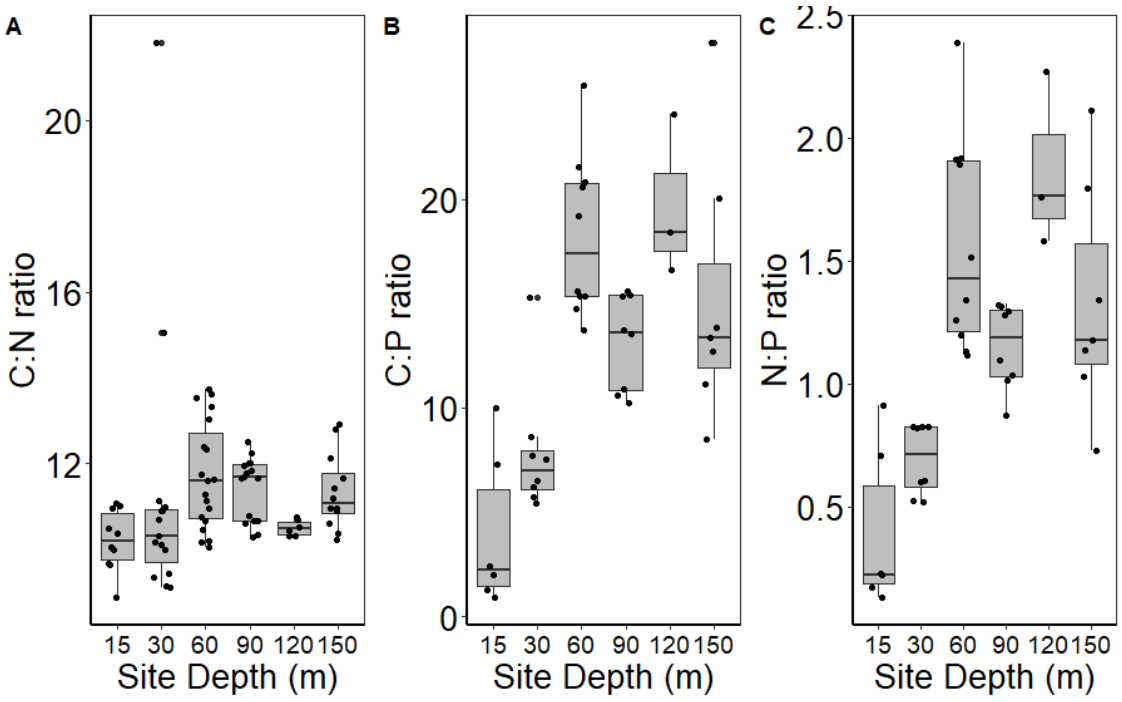

Figure 10. Sediment chemistry by site depth. A. C:N B. C:P C. N:P. Boxplots show median, and 25% quartiles. Points represent individual samples.

Table 14. Results of Tukey HSD pairwise tests for TC.

	15	30	60	90	120
30	0.52				
60	**<0.0001**	**<0.0001**			
90	**<0.0001**	**<0.0001**	0.47		
120	**<0.0001**	**<0.0001**	**0.023**	0.43	
150	**<0.0001**	**<0.0001**	0.68	1.00	0.40

Table 15. Results of Tukey HSD pairwise tests for TN.

	15	30	60	90	120
30	0.70				
60	**<0.0001**	**<0.0001**			
90	**<0.0001**	**<0.0001**	0.36		
120	**<0.0001**	**<0.0001**	**0.00051**	0.055	
150	**<0.0001**	**<0.0001**	0.60	1.00	**0.048**

Table 16. Results of Tukey HSD pairwise tests for TP.

	15	30	60	90	120
30	0.84				
60	**0.00059**	**<0.0001**			
90	**<0.0001**	**<0.0001**	**<0.0001**		
120	**<0.0001**	**<0.0001**	0.057	**0.022**	
150	**<0.0001**	**<0.0001**	**<0.0001**	0.24	0.78

Table 17. Results of Tukey HSD pairwise tests for C:P.

	15	30	60	90	120
30	0.49				
60	**<0.0001**	**<0.0001**			
90	**0.0021**	0.12	0.11		
120	**<0.0001**	**0.0015**	0.99	0.19	
150	**0.00019**	**0.013**	0.68	0.91	0.62

Table 18. Results of Tukey HSD pairwise tests for N:P.

	15	30	60	90	120
30	0.60				
60	**<0.0001**	**<0.0001**			
90	**0.0027**	0.098	0.14		
120	**<0.0001**	**0.0015**	0.75	**0.040**	
150	**0.00026**	**0.011**	0.72	0.91	0.22

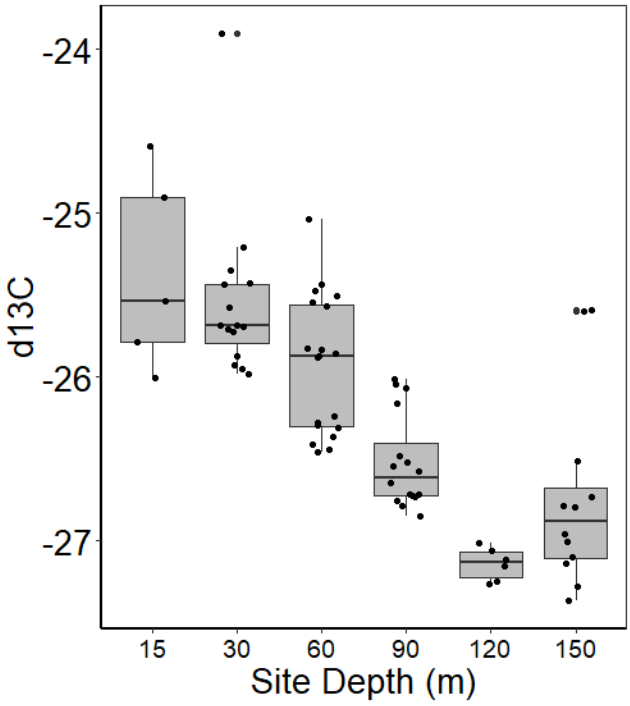

Figure 11. $\delta^{13}C$ from EA-IRMS. Boxplots show median, and 25% quartiles. Points represent individual samples.

Table 19. Results of Tukey HSD pairwise tests for $\delta^{13}C$.

	15	30	60	90	120
30	0.97				
60	0.13	0.134			
90	**<0.0001**	**<0.0001**	**0.0027**		
120	**<0.0001**	**<0.0001**	**<0.0001**	0.052	
150	**<0.0001**	**<0.0001**	**<0.0001**	0.80	0.46

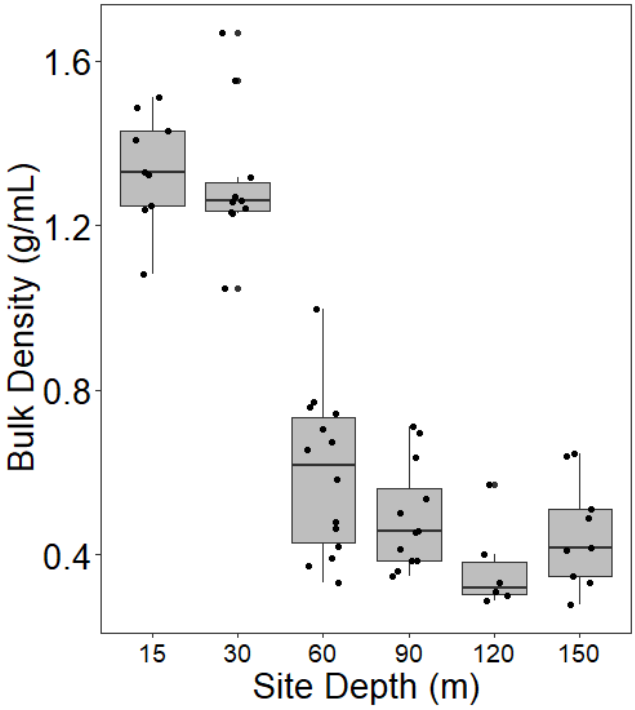

Figure 12. Bulk density of surficial sediment. Boxplots show median, and 25% quartiles. Points represent individual samples.

Table 20. Results of Tukey HSD pairwise tests for Bulk Density (g/mL).

	15	30	60	90	120
30	1.00				
60	**<0.0001**	**<0.0001**			
90	**<0.0001**	**<0.0001**	0.51		
120	**<0.0001**	**<0.0001**	**0.041**	0.61	
150	**<0.0001**	**<0.0001**	0.27	0.99	0.90

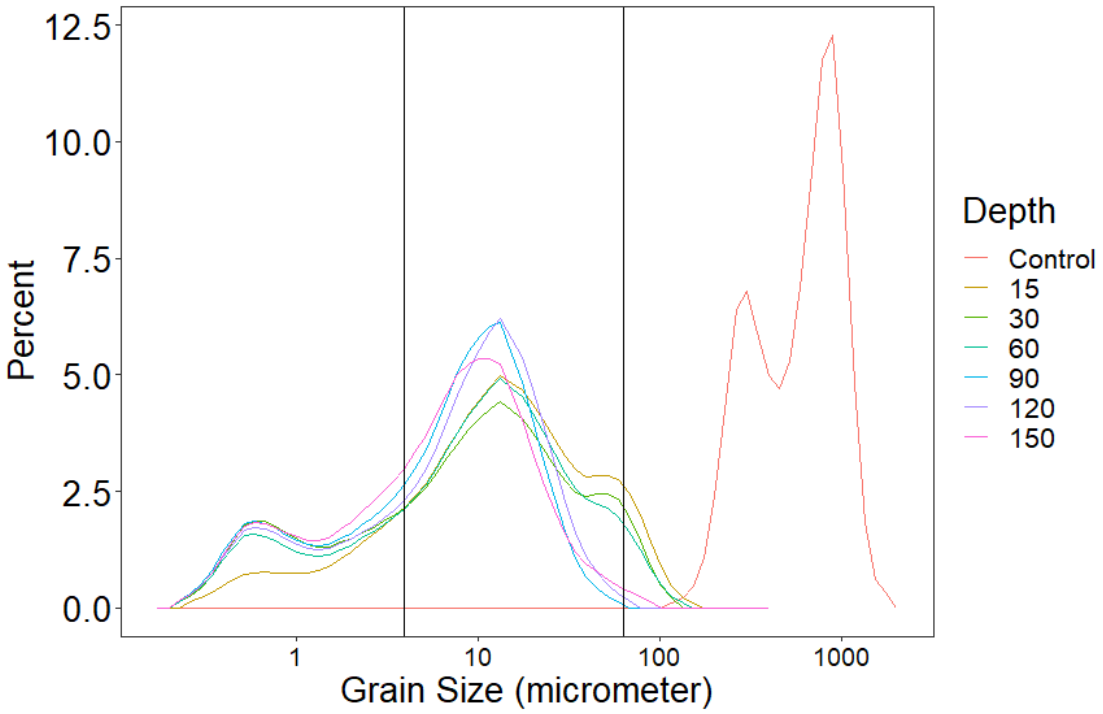

Figure 13. Percent of representative sample of a given grain size for different water depths (m). Vertical bars represent break points between clay (<2μm), silt (2-50μm), and sand (50-2000μm).

Table 21. Summary statistics for grain size analysis using GRADISTAT program.

Depth	Classification	Mode (1)	Mode (2)	Mean	Sorting	Sorting	Skew	Skew	Kurtosis	D_{10}	D_{50}	D_{90}
Control	Coarse Sand	954.8	322.4	599.3	Moderately	1.80	Fine	-0.29	0.74	269.4	681.6	1127.6
15	Medium Silt	14.21	55.21	12.93	Poorly	3.72	Fine	-0.15	1.12	2.022	13.83	60.03
30	Medium Silt	14.21	55.21	8.04	Very Poorly	4.71	Fine	-0.23	0.96	0.798	10.47	50.87
60	Medium Silt	14.21	0.627	8.74	Very Poorly	4.31	Fine	-0.25	1.076	0.883	11.17	47.45
90	Fine Silt	14.21	0.627	5.87	Poorly	3.55	Very Fine	-0.38	0.994	0.768	8.248	22.57
120	Fine Silt	14.21	0.627	6.68	Poorly	3.63	Very Fine	-0.39	1.024	0.821	9.405	25.96
150	Fine Silt	12.41	0.627	5.74	Poorly	3.63	Fine	-0.29	1.005	0.790	7.535	24.12

Bibliography

Agresti, A. (2007). An Introduction to Categorical Data Analysis, 2nd edition [Article]. In *Biometrics* (Issue 4). Wiley-Interscience. https://doi.org/10.1111/j.1541-0420.2007.00905_16.x

Ankar, S. (1977). The soft bottom ecosystem of the northern Baltic proper with special reference to the macrofauna. [Article]. *Contributions Asko Lab, No. 19*, 1.

Auer, M. T., Auer, N. A., Urban, N. R., & Auer, T. (2013). Distribution of the Amphipod Diporeia in Lake Superior: The Ring of Fire. *Journal of Great Lakes Research*, *39*, 33–46. https://doi.org/10.1016/j.jglr.2012.12.020

Auer, N. A., Cannon, B. A., & Auer, M. T. (2009). Life history, distribution, and production of Diporeia near the Keweenaw Peninsula Lake Superior. *Journal of Great Lakes Research*, *35*(4), 579–590. https://doi.org/10.1016/j.jglr.2009.08.004

Auer, N. A., & Kahn, J. E. (2004). Abundance and Distribution of Benthic Invertebrates, with Emphasis on Diporeia, along the Keweenaw Peninsula, Lake Superior. *Journal of Great Lakes Research*, *30*(SUPPL. 1), 340–359. https://doi.org/10.1016/S0380-1330(04)70396-2

Balcer, M. D. , K. N. , D. S. (1984). *Zooplankton of the Great Lakes : a guide to the identification and ecology of the common crustacean species* (N. L. Korda & S. I. Dodson, Eds.) [Book]. University of Wisconsin Press.

Barbiero, R. P., Schmude, K., Lesht, B. M., Riseng, C. M., Warren, G. J., & Tuchman, M. L. (2011). Trends in Diporeia populations across the Laurentian Great Lakes, 1997–2009. *Journal of Great Lakes Research*, *37*, 9–17. https://doi.org/10.1016/j.jglr.2010.11.009

Beisel, J.-N., Usseglio-Polatera, P., Thomas, S., & Moreteau, J.-C. (1998). Stream community structure in relation to spatial variation: the influence of mesohabitat characteristics. In *Hydrobiologia* (Vol. 389). https://doi.org/DOI: 10.1023/A:1003519429979

Bianchi, T. S., & Canuel, E. A. (2011). Stable Isotopes and Radiocarbon. In *Chemical Biomarkers in Aquatic Ecosystems* (pp. 30–48). Princeton University Press.

Blott, S. J., & Pye, K. (2001). GRADISTAT: a grain size distribution and statistics package for the analysis of unconsolidated sediments. *Earth Surface Processes and Landforms*, *26*(11), 1237–1248. https://doi.org/10.1002/esp.261

Bousfield, E. L. (1989). Revised Morphological Relationships Within the Amphipod Genera *Pontoporeia* and *Gammaracanthus* and the "Glacial Relict" Significance of their Postglacial Distributions. *Canadian Journal of Fisheries and Aquatic Sciences*, *46*(10), 1714–1725. https://doi.org/10.1139/f89-217

Bronte, C. R., Ebener, M. P., Schreiner, D. R., DeVault, D. S., Petzold, M. M., Jensen, D. A., Richards, C., & Lozano, S. J. (2003). Fish community change in Lake Superior, 1970–2000. *Canadian Journal of Fisheries and Aquatic Sciences*, *60*(12), 1552–1574. https://doi.org/10.1139/f03-136

Burlakova, L. E., Barbiero, R. P., Karatayev, A. Y., Daniel, S. E., Hinchey, E. K., & Warren, G. J. (2018). The benthic community of the Laurentian Great Lakes: Analysis of spatial gradients and temporal trends from 1998 to 2014. *Journal of Great Lakes Research*, *44*(4), 600–617. https://doi.org/10.1016/j.jglr.2018.04.008

Chícharo, M., & Chícharo, L. (2008). RNA:DNA Ratio and Other Nucleic Acid Derived Indices in Marine Ecology. *International Journal of Molecular Sciences*, *9*(8), 1453–1471. https://doi.org/10.3390/ijms9081453

Cook, David G., & Johnson, M. G. (1974). Benthic Macroinvertebrates of the St. Lawrence Great Lakes. *Journal of the Fisheries Research Board of Canada*, *31*(5), 763–782. https://doi.org/10.1139/f74-101

Cook, D.G. (1975). A preliminary report on the benthic macroinvertebrates of Lake Superior. *Journal of the Fisheries Research Board of Canada, Rep. 572*.

Corcoran, Margaret, Sherif, M. I., Smalley, C., Li, A., Rockne, K. J., Giesy, J. P., & Sturchio, N. C. (2018). Accumulation rates, focusing factors, and chronologies from depth profiles of 210Pb and 137Cs in sediments of the Laurentian Great Lakes. *Journal of Great Lakes Research*, *44*(4), 693–704. https://doi.org/10.1016/j.jglr.2018.05.013

Corcoran, Miles, Auer, N. A., & Auer, M. T. (2015). Measuring the effects of food availability on Lake Superior Diporeia consumption rates using radiolabeled algae. *Journal of Great Lakes Research*, *41*(2), 510–515. https://doi.org/10.1016/j.jglr.2015.03.026

Cummins, K. W., & Lauff, G. H. (1969). The influence of substrate particle size on the microdistribution of stream macrobenthos. *Hydrobiologia*, *34*(2), 145–181. https://doi.org/10.1007/BF00141925

Dermott, R. (2001). Sudden Disappearance of the Amphipod Diporeia from Eastern Lake Ontario, 1993–1995. *Journal of Great Lakes Research*, *27*(4), 423–433. https://doi.org/10.1016/S0380-1330(01)70657-0

Dermott, R., & Corning, K. (1988). Seasonal Ingestion Rates of *Pontoporeia hoyi* (Amphipoda) in Lake Ontario. *Canadian Journal of Fisheries and Aquatic Sciences*, *45*(11), 1886–1895. https://doi.org/10.1139/f88-220

Dermott, R., & Kerec, D. (1997). Changes to the deepwater benthos of eastern Lake Erie since the invasion of Dreissena: 1979-1993; *Canadian Journal of Fisheries and Aquatic Sciences*, *54*(4), 922–930. https://doi.org/10.1139/cjfas-54-4-922

Dermott, R., Munawar, M., Bonnell, R., Carou, S., Niblock, H., Nalepa, T. F., & Messick, G. (2005). *Preliminary Investigations for Causes of the Disappearance of Diporeia spp. from Lake Ontario*.

Dobiesz, N. E., McLeish, D. A., Eshenroder, R. L., Bence, J. R., Mohr, L. C., Ebener, M. P., Nalepa, T. F., Woldt, A. P., Johnson, J. E., Argyle, R. L., & Makarewicz, J. C. (2005). Ecology of the Lake Huron fish community, 1970-1999. *Canadian Journal of Fisheries and Aquatic Sciences*, *62*(6), 1432–1451. https://doi.org/10.1139/f05-061

Edlund, M. B., Jude, D. J., & Nalepa, T. F. (2021). Diets of the benthic amphipod Diporeia in southern Lake Michigan before and after the dreissenid invasion. *Journal of Great Lakes Research*, *47*(2), 447–462. https://doi.org/10.1016/j.jglr.2021.01.018

Evans, M. S., Quigley, M. A., & Wojcik, J. A. (1990). Comparative Ecology of Pontoporeia Hoyi Populations in Southern Lake Michigan: The Profundal Region Versus the Slope and Shelf Regions. *Journal of Great Lakes Research*, *16*(1), 27–40. https://doi.org/10.1016/S0380-1330(90)71396-2

Fahnenstiel, G. L., Sayers, M. J., Shuchman, R. A., Yousef, F., & Pothoven, S. A. (2016). Lake-wide phytoplankton production and abundance in the Upper Great Lakes: 2010–2013. *Journal of Great Lakes Research*, *42*(3), 619–629. https://doi.org/10.1016/j.jglr.2016.02.004

Fitzgerald, S. A., & Gardner, W. S. (1993). An algal carbon budget for pelagic-benthic coupling in Lake Michigan. *Limnology and Oceanography*, *38*(3), 547–560. https://doi.org/10.4319/lo.1993.38.3.0547

Folk, R. L., & Ward, W. C. (1957). Brazos River bar [Texas]; a study in the significance of grain size parameters. *Journal of Sedimentary Research*, *27*(1), 3–26. https://doi.org/10.1306/74D70646-2B21-11D7-8648000102C1865D

Gamble, A. E., Hrabik, T. R., Yule, D. L., & Stockwell, J. D. (2011). Trophic connections in Lake Superior Part II: The nearshore fish community. *Journal of Great Lakes Research*, *37*, 550–560. https://doi.org/10.1016/j.jglr.2011.06.008

Gardner, W. S., Nalepa, T. F., Frez, W. A., Cichocki, E. A., & Landrum, P. F. (1985). Seasonal Patterns in Lipid Content of Lake Michigan Macroinvertebrates. *Canadian Journal of Fisheries and Aquatic Sciences*, *42*(11), 1827–1832. https://doi.org/10.1139/f85-229

Gardner, W. S., Quigley, M. A., Fahnenstiel, G. L., Scavia, D., & Frez, W. A. (1990). *Pontoporeia hoyi—a Direct Trophic Link between Spring Diatoms and Fish in Lake Michigan* (pp. 632–644). https://doi.org/10.1007/978-3-642-84077-7_34

Gauvin, J. M., Gardner, W. S., & Quigley, M. A. (1989). Effects of Food Removal on Nutrient Release Rates and Lipid Content of Lake Michigan Pontoporeia hoyi. *Canadian Journal of Fisheries and Aquatic Sciences*, *46*(7), 1125–1130. https://doi.org/10.1139/f89-146

Gossiaux, D. C., Landrum, P. F., & Tsymbal, V. N. (1992). Response of the Amphipod Diporeia spp. to Various Stressors: Cadmium, Salinity, and Temperature. *Journal of Great Lakes Research*, *18*(3), 364–371. https://doi.org/10.1016/S0380-1330(92)71304-5

Green, R. H. (1968). A Summer-Breeding Population of the Relict Amphipod Pontoporeia affinis Lindström. *Oikos*, *19*(2), 191. https://doi.org/10.2307/3565006

Griffiths, R. W., Schloesser, D. W., Leach, J. H., & Kovalak, W. P. (1991). Distribution and Dispersal of the Zebra Mussel (*Dreissena polymorpha*) in the Great Lakes Region. *Canadian Journal of Fisheries and Aquatic Sciences*, *48*(8), 1381–1388. https://doi.org/10.1139/f91-165

Grigorovich, I. A., Kelly, J. R., Darling, J. A., & West, C. W. (2008). The Quagga Mussel Invades the Lake Superior Basin. *Journal of Great Lakes Research*, *34*(2), 342–350. https://doi.org/10.3394/0380-1330

Guiguer, K. R. R. A., & Barton, D. R. (2002). The Trophic Role of Diporeia (Amphipoda) in Colpoys Bay (Georgian Bay) Benthic Food Web: A Stable Isotope Approach. *Journal of Great Lakes Research*, *28*(2), 228–239. https://doi.org/10.1016/S0380-1330(02)70579-0

Harkey, G. A., Lydy, M. J., Kukkonen, J., & Landrum, P. F. (1994). Feeding selectivity and assimilation of PAH and PCB in *Diporeia* spp. *Environmental Toxicology and Chemistry*, *13*(9), 1445–1455. https://doi.org/10.1002/etc.5620130908

Hebert, P. D. N., Muncaster, B. W., & Mackie, G. L. (1989). Ecological and Genetic Studies on *Dreissena polymorpha* (Pallas): a New Mollusc in the Great Lakes.

Canadian Journal of Fisheries and Aquatic Sciences, *46*(9), 1587–1591. https://doi.org/10.1139/f89-202

Heinen, E. A., & McManus, J. (2004). Carbon and Nutrient Cycling at the Sediment-water Boundary in Western Lake Superior. *Journal of Great Lakes Research*, *30*, 113–132. https://doi.org/10.1016/S0380-1330(04)70381-0

Hewson, I., Eaglesham, J. B., Höök, T. O., LaBarre, B. A., Sepúlveda, M. S., Thompson, P. D., Watkins, J. M., & Rudstam, L. G. (2013). Investigation of viruses in Diporeia spp. from the Laurentian Great Lakes and Owasco Lake as potential stressors of declining populations. *Journal of Great Lakes Research*, *39*(3), 499–506. https://doi.org/10.1016/J.JGLR.2013.06.006

Howell, E. T., Chomicki, K. M., & Kaltenecker, G. (2012). Patterns in water quality on Canadian shores of Lake Ontario: Correspondence with proximity to land and level of urbanization. *Journal of Great Lakes Research*, *38*(SUPPL.4), 32–46. https://doi.org/10.1016/j.jglr.2011.12.005

IJC. International Joint Commission. (1987). *Revised Great Lakes Water Quality Agreement of 1978, as Amended by Protocol, Signed November 18, 1987*. .

Kainz, M. J., Johannsson, O. E., & Arts, M. T. (2010). Diet effects on lipid composition, somatic growth potential, and survival of the benthic amphipod Diporeia spp. *Journal of Great Lakes Research*, *36*(2), 351–356. https://doi.org/10.1016/j.jglr.2010.02.004

Karatayev, A. Y., Burlakova, L. E., & Padilla, D. K. (2002). Impacts of Zebra Mussels on Aquatic Communities and their Role as Ecosystem Engineers. In *Invasive Aquatic Species of Europe. Distribution, Impacts and Management* (pp. 433–446). Springer Netherlands. https://doi.org/10.1007/978-94-015-9956-6_43

Kemp, A. L. W., Dell, C. I., & Harper, N. S. (1978). Sedimentation Rates and a Sediment Budget for Lake Superior. *Journal of Great Lakes Research*, *4*(3–4), 276–287. https://doi.org/10.1016/S0380-1330(78)72198-2

Korbel, K. L., Stephenson, S., & Hose, G. C. (2019). Sediment size influences habitat selection and use by groundwater macrofauna and meiofauna. *Aquatic Sciences*, *81*(2), 39. https://doi.org/10.1007/s00027-019-0636-1

Kraft, K. J. (1979). Pontoporeia Distribution Along the Keweenaw Shore of Lake Superior Affected by Copper Tailings. *Journal of Great Lakes Research*, *5*(1), 28–35. https://doi.org/10.1016/S0380-1330(79)72124-1

Lafrancois, T., Hove, M., & McCartney, M. A. (2019). *Mussel survey and population assessment, 2017. Apostle Islands National Lakeshore. Natural Resources Report NPS/APIS/NRR-2019/1867*.

Landrum, P. F., Dupuis, W. S., & Kukkonen, J. (1994). Toxicokinetics and toxicity of sediment-associated pyrene and phenanthrene in *Diporeia* spp.: Examination of equilibrium-partitioning theory and residue-based effects for assessing hazard. *Environmental Toxicology and Chemistry*, *13*(11), 1769–1780. https://doi.org/10.1002/etc.5620131108

Landrum, P. F., Gossiaux, D. C., Nalepa, T. F., & Fanslow, D. L. (2000). Evaluation of Lake Michigan Sediment For Causes of the Disappearance of Diporeia spp. in Southern Lake Michigan. *Journal of Great Lakes Research*, *26*(4), 402–407. https://doi.org/10.1016/S0380-1330(00)70703-9

Landrum, P. F., Lotufo, G. R., Gossiaux, D. C., Gedeon, M. L., & Lee, J.-H. (2003). Bioaccumulation and critical body residue of PAHs in the amphipod, Diporeia spp.: additional evidence to support toxicity additivity for PAH mixtures. *Chemosphere*, *51*(6), 481–489. https://doi.org/10.1016/S0045-6535(02)00863-9

Landrum, P. F., & Nalepa, T. F. (1998). A Review of the Factors Affecting the Ecotoxicology of Diporeia spp. *Journal of Great Lakes Research*, *24*(4), 889–904. https://doi.org/10.1016/S0380-1330(98)70870-6

Landrum, P., & Faust, W. (1991). Effect of Variation in Sediment Composition on the Uptake Rate Coefficient for Selected PCB and PAH Congeners by the Amphipod,. In *Aquatic Toxicology and Risk Assessment: Fourteenth Volume* (pp. 263-263–17). ASTM International. https://doi.org/10.1520/STP23577S

Levinton, J. S. (1995). *Marine biology: function, biodiversity, ecology*. Oxford University Press. https://doi.org/10.1017/S0025315400030812

Li, J., Crowe, S. A., Miklesh, D., Kistner, M., Canfield, D. E., & Katsev, S. (2012). Carbon mineralization and oxygen dynamics in sediments with deep oxygen penetration, Lake Superior. *Limnology and Oceanography*, *57*(6), 1634–1650. https://doi.org/10.4319/lo.2012.57.6.1634

Lozano, S. J., Gedeon, M. L., & Landrum, P. F. (2003). The Effects of Temperature and Organism Size on the Feeding Rate and Modeled Chemical Accumulation in Diporeia spp. for Lake Michigan Sediments. *Journal of Great Lakes Research*, *29*(1), 79–88. https://doi.org/10.1016/S0380-1330(03)70417-1

Madenjian, C. P., Pothoven, S. A., Schneeberger, P. J., Ebener, M. P., Mohr, L. C., Nalepa, T. F., & Bence, J. R. (2010). Dreissenid mussels are not a "dead end" in Great Lakes food webs. *Journal of Great Lakes Research*, *36*, 73–77. https://doi.org/10.1016/j.jglr.2009.09.001

Makarewicz, J. C., & Lewis, T. W. (2015). Exploring spatial trends and causes in Lake Ontario coastal chemistry: Nutrients and pigments. *Journal of Great Lakes Research*, *41*(3), 794–800. https://doi.org/10.1016/j.jglr.2015.04.011

Manly, B. F. J. (1993). *Resource selection by animals : statistical design and analysis for field studies* (L. L. McDonald & D. L. Thomas, Eds.; 1st ed..) [Book]. Chapman & Hall.

Marzolf, G. R. (1965). Substrate Relations of the Burrowing Amphipod Pontoporeia Affinis in Lake Michigan. *Ecology*, *46*(5), 579–592. https://doi.org/10.2307/1934998

Masclaux, H., & Richoux, N. B. (2017). Effects of temperature and food quality on isotopic turnover and discrimination in a cladoceran. *Aquatic Ecology*, *51*(1), 33–44. https://doi.org/10.1007/s10452-016-9592-1

Mehler, K., Burlakova, L. E., Karatayev, A. Y., & Scharold, J. (2018). *Major Findings from the CSMI Benthic Macroinvertebrate Survey in Lake Superior in 2016 with an Emphasis on Temporal Trends. Lake Superior Benthos: Cooperative Science and Monitoring Initiative, Final Report. USGS-GLRI G14AC00263.* http://greatlakescenter.buffalostate.edu/sites/greatlakescenter.buffalostate.edu/files/uploads/Documents/Publications/LakeSuperiorBenthos_CSMI2016_FinalReport.pdf

Messick, G., Overstreet, R., Nalepa, T., & Tyler, S. (2004). Prevalence of parasites in amphipods Diporeia spp. from Lakes Michigan and Huron, USA. *Diseases of Aquatic Organisms*, *59*, 159–170. https://doi.org/10.3354/dao059159

Meyers, P. A. (1997). Organic geochemical proxies of paleoceanographic, paleolimnologic, and paleoclimatic processes [Article]. *Organic Geochemistry*, *27*(5–6), 213–250. https://doi.org/10.1016/S0146-6380(97)00049-1

Mills, E. L., Chrisman, J. R., Baldwin, B., Owens, R. W., O'Gorman, R., Howell, T., Roseman, E. F., & Raths, M. K. (1999). Changes in the Dreissenid Community in the Lower Great Lakes with Emphasis on Southern Lake Ontario. *Journal of Great Lakes Research*, *25*(1), 187–197. https://doi.org/10.1016/S0380-1330(99)70727-6

Mills, E. L., Dermott, R. M., Roseman, E. F., Dustin, D., Mellina, E., Conn, D. B., & Spidle, A. P. (1993). Colonization, Ecology, and Population Structure of the "Quagga''' Mussel (Bivalvia: Dreissenidae) in the Lower Great Lakes." *Canadian Journal of Fisheries and Aquatic Sciences*, *50*(11), 2305–2314. https://doi.org/10.1139/f93-255

Montefalcone, M., Parravicini, V., & Bianchi, C. N. (2011). Quantification of Coastal Ecosystem Resilience. In *Treatise on Estuarine and Coastal Science* (Vol. 10, pp. 49–70). Elsevier. https://doi.org/10.1016/B978-0-12-374711-2.01003-2

Munawar, I. F., & Munawar, M. (2009). Phytoplankton Communities of Lake Superior, 2001: Changing species composition and biodiversity of a pristine ecosystem. In M. Munawar & I. F. Munawar (Eds.), *State of Lake Superior* (pp. 319–360). Michigan State University Press. http://www.jstor.org/stable/10.14321/j.ctt13x0pcx.16

Nalepa, T. F. (1989). Estimates of Macroinvertebrate Biomass in Lake Michigan. *Journal of Great Lakes Research*, *15*(3), 437–443. https://doi.org/10.1016/S0380-1330(89)71499-4

Nalepa, T. F., Fanslow, D. L., & Foley, A. J. (2005). Spatial patterns in population trends of the amphipod *Diporeia* spp. and *Dreissena* mussels in Lake Michigan. *SIL Proceedings, 1922-2010*, *29*(1), 426–431. https://doi.org/10.1080/03680770.2005.11902048

Nalepa, T. F., Fanslow, D. L., Foley III, A. J., Lang, G. A., Eadie, B. J., & Quigley, M. A. (2006). Continued disappearance of the benthic amphipod *Diporeia* spp. in Lake Michigan: is there evidence for food limitation? *Canadian Journal of Fisheries and Aquatic Sciences*, *63*(4), 872–890. https://doi.org/10.1139/f05-262

Nalepa, T. F., Fanslow, D. L., & Lang, G. A. (2009). Transformation of the offshore benthic community in Lake Michigan: recent shift from the native amphipod *Diporeia* spp. to the invasive mussel *Dreissena rostriformis bugensis*. *Freshwater Biology*, *54*(3), 466–479. https://doi.org/10.1111/j.1365-2427.2008.02123.x

Nalepa, T. F., Hartson, D. J., Buchanan, J., Cavaletto, J. F., Lang, G. A., & Lozano, S. J. (2000). Spatial variation in density, mean size and physiological condition of the holarctic amphipod *Diporeia* spp. in Lake Michigan. *Freshwater Biology*, *43*(1), 107–119. https://doi.org/10.1046/j.1365-2427.2000.00530.x

Nalepa, T. F., Hartson, D. J., Fanslow, D. L., Lang, G. A., & Lozano, S. J. (1998). Declines in benthic macroinvertebrate populations in southern Lake Michigan, 1980-1993. *Canadian Journal of Fisheries and Aquatic Sciences*, *55*(11), 2402–2413. https://doi.org/10.1139/f98-112

Nalepa, T. F., Schloesser, D. W., Pothoven, S. A., Hondorp, D. W., Fanslow, D. L., Tuchman, M. L., & Fleischer, G. W. (2001). First Finding of the Amphipod Echinogammarus ischnus and the Mussel Dreissena bugensis in Lake Michigan.

Journal of Great Lakes Research, *27*(3), 384–391. https://doi.org/10.1016/S0380-1330(01)70653-3

Nel, R., McLachlan, A., & Winter, D. P. E. (2001). The effect of grain size on the burrowing of two Donax species. *Journal of Experimental Marine Biology and Ecology*, *265*(2), 219–238. https://doi.org/10.1016/S0022-0981(01)00335-5

Pilgrim, E. M., Scharold, J. v., Darling, J. A., & Kelly, J. R. (2009). Genetic structure of the benthic amphipod Diporeia (Amphipoda: Pontoporeiidae) and its relationship to abundance in Lake Superior. *Canadian Journal of Fisheries and Aquatic Sciences*, *66*(8), 1318–1327. https://doi.org/10.1139/F09-086

Pothoven, S. A., & Madenjian, C. P. (2008). Changes in Consumption by Alewives and Lake Whitefish after Dreissenid Mussel Invasions in Lakes Michigan and Huron. *North American Journal of Fisheries Management*, *28*(1), 308–320. https://doi.org/10.1577/M07-022.1

Pothoven, S. A., & Nalepa, T. F. (2006). Feeding Ecology of Lake Whitefish in Lake Huron [Article]. *Journal of Great Lakes Research*, *32*(3), 489–501. https://doi.org/10.3394/0380-1330(2006)32[489:FEOLWI]2.0.CO;2

Quigley, M. A. (1988). GUT FULLNESS OF THE DEPOSIT-FEEDING AMPHIPOD, PONTOPOREIA HOYI, IN SOUTHEASTERN LAKE MICHIGAN. *Journal of Great Lakes Research*, *14*(2), 178–187. https://doi.org/10.1016/S0380-1330(88)71547-6

Quigley, M. A., & Vanderploeg, H. A. (1991). Ingestion of live filamentous diatoms by the Great Lakes amphipod, Diporeia sp.: a case study of the limited value of gut contents analysis. *Hydrobiologia*, *223*, 141–148. https://link-springer-com.ezp2.lib.umn.edu/content/pdf/10.1007%2FBF00047635.pdf

Quinn, G. P., & Keough, M. J. (2003). *Experimental design and data analysis for biologists*. Cambridge University Press.

Reeders, H. H., & Bij de Vaate, A. (1992). Bioprocessing of polluted suspended matter from the water column by the zebra mussel (Dreissena polymorpha Pallas). *Hydrobiologia*, *239*(1), 53–63. https://doi.org/10.1007/BF00027529

Rennie, M. D., Sprules, W. G., & Johnson, T. B. (2009). Factors affecting the growth and condition of lake whitefish (Coregonus clupeaformis) [Article]. *Canadian Journal of Fisheries and Aquatic Sciences*, *66*(12), 2096–2108. https://doi.org/10.1139/F09-139

Richter, L., Schwenkmezger, L., Becker, J., Winkelmann, C., Hellmann, C., & Worischka, S. (2018). The very hungry amphipod: the invasive Dikerogammarus villosus shows high consumption rates for two food sources and independent of predator cues. *Biological Invasions*, *20*(5), 1321–1335. https://doi.org/10.1007/s10530-017-1629-4

Roe, S. L., & MacIsaac, H. J. (1997). Deepwater population structure and reproductive state of quagga mussels (Dreissena bugensis) in Lake Erie [Article]. *Canadian Journal of Fisheries and Aquatic Sciences*, *54*(10), 2428–2433. https://doi.org/10.1139/cjfas-54-10-2428

Rudstam, L. G. (1989). A bioenergetic model for *Mysis* growth and consumption applied to a Baltic population of *Mysis mixta*. *Journal of Plankton Research*, *11*(5), 971–983. https://doi.org/10.1093/plankt/11.5.971

Ryan, D. J., Sepúlveda, M. S., Nalepa, T. F., & Höök, T. O. (2012). Spatial variation in RNA:DNA ratios of Diporeia spp. in the Great Lakes region. *Journal of Great Lakes Research*, *38*(2), 187–195. https://doi.org/10.1016/j.jglr.2012.01.007

Scharold, J. V., Lozano, S. J., & Corry, T. D. (2009). Status of benthic macroinvertebrates in southern nearshore Lake Superior, 1994-2003. In M. Munawar & I. F. Munawar (Eds.), *State of Lake Superior* (pp. 473–492). Aquatic Ecosystem Health and Management Society. Ecovision World Monograph Series.

Scharold, J. v., & Corry, T. D. (2021). Status of the amphipod Diporeia spp. in Lake Superior, 2006–2016. *Journal of Great Lakes Research*. https://doi.org/10.1016/j.jglr.2021.04.013

Scharold, J. v., Lozano, S. J., & Corry, T. D. (2004). Status of the Amphipod Diporeia spp. in Lake Superior, 1994–2000. *Journal of Great Lakes Research*, *30*(1), 360–368. https://doi.org/10.1016/S0380-1330(04)70397-4

Sierszen, M. E., Hrabik, T. R., Stockwell, J. D., Cotter, A. M., Hoffman, J. C., & Yule, D. L. (2014). Depth gradients in food-web processes linking habitats in large lakes: Lake Superior as an exemplar ecosystem. *Freshwater Biology*, *59*(10), 2122–2136. https://doi.org/10.1111/fwb.12415

Sierszen, M. E., Peterson, G. S., & Scharold, J. v. (2006). Depth-specific patterns in benthic–planktonic food web relationships in Lake Superior. *Canadian Journal of Fisheries and Aquatic Sciences*, *63*(7), 1496–1503. https://doi.org/10.1139/f06-057

Sly, P. G., & Christie, W. J. (1992). Factors influencing densities and distributions of Pontoporeia hoyi in Lake Ontario. *Hydrobiologia*, *235–236*(1), 321–352. https://doi.org/10.1007/BF00026224

Smith, C. K., & Petranka, J. W. (1987). Prey size-distributions and size-specific foraging success of Ambystoma larvae. *Oecologia*, *71*(2), 239–244. https://doi.org/10.1007/BF00377290

Souffreau, C., Vanormelingen, P., Verleyen, E., Sabbe, K., & Vyverman, W. (2010). Tolerance of benthic diatoms from temperate aquatic and terrestrial habitats to experimental desiccation and temperature stress. *Phycologia*, *49*(4), 309–324. https://doi.org/10.2216/09-30.1

Sterner, R. W. (2010). In situ-measured primary production in Lake Superior. *Journal of Great Lakes Research*, *36*(1), 139–149. https://doi.org/10.1016/j.jglr.2009.12.007

Sterner, R. W. (2021). The Laurentian Great Lakes: A Biogeochemical Test Bed. *Annual Review of Earth and Planetary Sciences*, *49*(1), 201–229. https://doi.org/10.1146/annurev-earth-071420-051746

Sun, T., Liu, C., Li, X., An, D., Yu, H., Ma, Z., & Liu, F. (2019). The effect of substrate grain size on burrowing ability and distribution characteristics of Perinereis aibuhitensis. *Acta Oceanologica Sinica*, *38*(12), 52–58. https://doi.org/10.1007/s13131-019-1348-z

ten Winkel, E. H., & Davids, C. (1982). Food selection by Dreissena polymorpha Pallas (Mollusca: Bivalvia). *Freshwater Biology*, *12*(6). https://doi.org/10.1111/j.1365-2427.1982.tb00647.x

Thomas, R. L. (1969). A note on the relationship of grain size, clay content, quartz and organic carbon in some Lake Erie and Lake Ontario sediments. *Journal of*

Sedimentary Research, *39*(2), 803–809. https://doi.org/10.1306/74D71D34-2B21-11D7-8648000102C1865D

Thomas, R. L., & Dell, C. I. (1978). Sediments of Lake Superior. *Journal of Great Lakes Research*, *4*(3–4), 264–275. https://doi.org/10.1016/S0380-1330(78)72197-0

Todd Howell, E., Marvin, C. H., Bilyea, R. W., Kauss, P. B., & Somers, K. (1996). Changes in Environmental Conditions During Dreissena Colonization of a Monitoring Station in Eastern Lake Erie. *Journal of Great Lakes Research*, *22*(3), 744–756. https://doi.org/10.1016/S0380-1330(96)70993-0

Urban, N. R., Lu, X., Chai, Y., & Apul, D. S. (2004). Sediment Trap Studies in Lake Superior: Insights into Resuspension, Cross-margin Transport, and Carbon Cycling. *Journal of Great Lakes Research*, *30*(SUPPL. 1), 147–161. https://doi.org/10.1016/S0380-1330(04)70383-4

Watkins, J. M., Rudstam, L. G., Mills, E. L., & Teece, M. A. (2012). Coexistence of the native benthic amphipod Diporeia spp. and exotic dreissenid mussels in the New York Finger Lakes. *Journal of Great Lakes Research*, *38*, 226–235. https://doi.org/10.1016/j.jglr.2012.02.001

Winnell, M. H., & White, D. S. (1984). Ecology of Shallow and Deep Water Populations of Pontoporeia hoyi (Smith) (Amphipoda) in Lake Michigan. *Freshwater Invertebrate Biology*, *3*(3), 118–138. https://doi.org/10.2307/1467186

Yurista, P., Kelly, J. R., & Miller, S. E. (2011). Lake Superior: Nearshore variability and a landscape driver concept. *Aquatic Ecosystem Health & Management*, *14*(4), 345–355. https://doi.org/10.1080/14634988.2011.624942